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ON THE NATURE OF THE BLAINI BOULDER BED

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Received November 5, 1942
(Communicated by Prof. L. Rama Rau, M.A., F.G.S., F.N.I., F.A.Sc.)

The Blaini conglomerates were first described by H. B. Medlicott in 1864 and were named by him after the stream near Solon where they were first observed. These conglomerates were described as containing boulders set in a fine grained slaty matrix, often in excess of the volume of pebbles. On the basis of surface markings on the pebbles Oldham concluded that these peculiar markings together with the nature of the boulders could only have been obtained through the agency of floating ice from which stones were dropped into the silt that was accumulating into the neighbouring sea. The conglomerate bed was therefore raised to the status of a Glacial Boulder Bed, a status which it is enjoying even to this day without question.

In the period when Medlicott and Oldham worked on the Himalayas, Fisher's ideas about the origin and structure of mountains were holding ground and the Himalayas were supposed to represent a gigantic but simple orthoclinal fold wherein as we proceeded northward we were supposed to meet older and older rocks. The succession was supposed to be perfectly normal with a few unconformities and disturbed only by some faulted dislocations. It was therefore difficult for these geologists to account for a boulder bed except as a normal continental formation marking interruption in sedimentation and the heterogeneity of boulders with surface scratching could be attributed only to glacial action.

The ideas of mountain structure have since then undergone a tremendous change and horizontal movements of one formation over another over enormous distances have been demonstrated. The mechanism of this horizontal translation would, it is clear, immediately bring in one more agency which is capable of giving rise to conglomerates of considerable magnitude.

Boulder beds of the Blaini type have been found in widely separated areas and for nearly every one of them a common origin through glacial action had been assigned. Thus the boulder beds of Simla Himalayas, Salt Range, Hazara, the Talchirs of Peninsular India, South Africa, Western Australia, New South Wales, etc., were all considered as of glacial origin

pointing to contemporaneous existence of enormous glaciers covering a large part of the Gondwana continent.

The dogmatism with which most of the Himalayan (pre-Siwalik) conglomerates have been correlated with the Permo-Carboniferous glaciation of Gondwana Land can only be attributed to the paucity of other explanations which could account for such enormous thickness of conglomerates.

When one remembers that in the Simla Himalayas, there is not only one but a number of conglomerate beds occurring associated with widely different types of rock-formations from highly metamorphosed to least metamorphosed sediments, a fact clearly recognised by all Himalayan workers, it is obvious that the hypothesis of Permo-Carboniferous glaciation cannot account for them all. Again in the absence of other, more direct evidences, it is difficult to choose the one boulder bed out of so many which is to be properly attributed to the Permo-Carboniferous Glaciation. On the other hand if a glacial origin of all these boulder beds were admitted a number of glacial epochs will have to be postulated at different periods of geological history of the Himalayan region. Holland has actually suggested that there have been many glacial periods even before Talchir age and that he would prefer to refer the Blaini Boulder Bed to one of the much older pre-Palæozoic glacial periods and place it under Purana group.[1]

The consequences of assuming a glacial origin of the 'Blaini Boulder Bed' are to a large extent, misleading and Auden recognised this ; for, in connection with the Mandhalis and their correlation with the Blaini Boulder Bed he writes:—

"I can offer no absolute proof that the view previously held namely that the boulder beds are glacial and all Blaini, is erroneous. But this former view has led to difficulties."[2]

On the other hand Wadia is impressed by the significance of these boulder beds. In connection with the conglomerates of the Poonch region he writes :

"Dr. Pilgrim was the first to recognise the boulder conglomerate found in the Betar valley as the basal Gondwana conglomerate, a relationship which I at first if not overlooked, had underestimated. Dr. Pilgrim realised the true significance of this stratum and foresaw in it a plane denoting an important horizon in Pir Panjal Geology. The presence of a coarse bouldery conglomerate at this horison with a fine grained matrix, immediately suggests

[1] *Rec. G. S. I.*, 37, Pt. 1, 129–35.
[2] *Ibid.*, 67, Pt. 4, 421.

its correlation with the glacial boulder bed of Talchirs of Peninsular India and the boulder bed at the base of the Upper Carboniferous of Salt Range." But he adds "none of the boulders bear clear traces of ice grooving, polishing or faceting."[3]

Wadia again refers to the importance of this Boulder Bed in his text-book on the geology of India where he states " In Hazara, N. W. Kashmir, and several areas of central Himalayas, the Upper Carboniferous Conglomerate is seen to overlie unconformably formations of far lower horizons whether Haimant, Silurian or Muth, all the intervening stages being missing. *This conglomerate is the most important horizon, a datum line in the geology of India, it covers an unconformity universal in all parts of India where Permian system is seen.*"[4]

It is thus clear that these 'boulder beds' or ' boulder conglomerates ' have been invested with an extraordinary importance in the Geology of India and it would be interesting to enquire if the evidences on which these far-reaching conclusions are based are altogether incontravertible. On the basis of certain field observations recently made by the author the question is now raised and it is hoped that a valuable discussion will follow which will serve to clarify the position.

Evidence of Pebbles in the Boulder Bed

When we study the lithology of this conglomerate bed, we see that it is composed for a large part of rolled quartz pebbles set in a slaty matrix. The pebbles, however, are not exclusively of any one type but include a variety of rock types in different proportions. Again, conglomerate beds in different localities have distinctive set of pebbles depending on the nature of associated rock formations. In spite of the variability of their constituent pebbles we find certain features about the nature and distribution of these pebbles which throw a flood of light on the possible mode of formation of the containing bed.

Oldham while describing the Mandhalis as a very complex group states[5] " The conglomerate bed is composed of fragments of rocks over which it rests and embedded in the matrix of the same rock in finely comminuted form."

Auden, discussing the evidence of pebbles in the Blaini conglomerate states " The boulders of Blaini are almost entirely dark slates, sandstones

[3] *Mem. G. S. I.*, **51**, Pt. 2, 245.
[4] Wadia, *Geology of India*, 1937, 114.
[5] *G. S. I.*, **21**, 136.

and quartzites, all types which can be matched in the Simla slates and Jaunsars."[6]

Looking at this almost exclusive nature of boulders it is difficult to explain the absence of other rock pebbles in a sedimentary conglomerate bed unless only two types of rock formations, the Simlas and Jaunsars, were exposed to denudation at the time of its formation. In the field the conglomerate band is seen to occur between the Simla slates and the Jaunsar quartzites. This means that the conglomerate beside containing pebbles of the Simla formation which is below it, also contains boulders of the Jaunsar formation which is above it. This is clearly impossible in a sedimentary conglomerate bed.

The fact that the provenance of pebble material is restricted to the rocks immediately below and above, can be explained only if we regard the intervening conglomerate as of the 'crush breccia' type.

Regarding the absence of older metamorphic rocks among the boulders Auden writes[7] "It is a striking fact that no single instance has been found either in the field or in the rock slice of any true schists or metamorphic rocks of meso-type being included in pre-Tertiary conglomerates." This complete absence of meso-metamorphic rocks as pebbles has been an enigma to all the Himalayan geologists and numerous explanations have been attempted. Auden has tried to explain this by postulating that the metamorphic rocks acquired their meso-character after the formation of the conglomerate bed.[8] It is however not explained how, when one rock formation suffered meso-metamorphism in some post-Blaini period, the associated Blaini bed could have escaped all metamorphic effects.

According to the present author the absence of such metamorphic rock pebbles in the conglomerate is due not to the absence of any metamorphosed rocks exposed to denudation at that period nor to any metamorphism at a later date but to the fact that these conglomerates were formed due to thrusting of Jaunsar quartzites over the Simla slates so that the pebble material was largely derived from these two rock types to the exclusion of other types, metamorphosed or otherwise, existing at the time of this 'boulder bed' formation.

The boulders in the Blaini conglomerate are however not restricted to older rock formations like the Simlas and Jaunsars; in places they also

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[6] *G. S. I.*, 67, 416.
[7] *Ibid.*, 67, 416.
[8] *Ibid.*, 67, 418.

include fragments of much younger formations like the Infra Krols, Krols, Dagshais and Tertiary Granites. In certain localities, as for example in the Neweli stream 4 miles due south of Chandpur hill, fragments of rocks lithologically indistinquishable from infra krol shales are extraordinarily abundant in the ' Blaini bed ' which Auden, in his map of the Krol belt, marks at the junction of the jaunsars and the overlying Infra-Krols.

Fragments of Deoban limestone have been noted among the boulders of the 'Blaini' by Oldham. He states[9] " In Northern Jaunsar and Bawar where it rests on the Deoban limestone fragments of that rock are extremely abundant in it and there are several beds of a conglomerate composed exclusively of rounded boulders of Deoban Limestone embedded in a matrix of the same rock in a finely comminuted form." Deoban limestone has all the lithological characters of Krol limestone with which it was long correlated. This similarity with Krol limestone was also appreciated by Pilgrim and West but the occurrence of Deoban boulders in the 'Blaini conglomerate' made them reject this correlation and decide the age of the Deoban Limestone as older than Blaini and as equivalent to Mandhalis of northern Chakrata. Regarding its relationship with the Jaunsars Auden states[10] "The same Deoban limestone rests on the Jaunsar series while, in the Beshair and Gutu Gads Jaunsars are found as well above the Deoban limestone." This reversal of relations in these localities is clearly a result of thrust contact as was already recognised by Auden. Any breccia developed along this thrust would naturally include boulders of Deoban limestone as well. The inclusion of this limestone therefore among boulders at this junction is no proof of its older age and hence there is no need to differentiate it on this account from the Krols with which it has all the characters in common.

Much younger rock types have also been noticed among the pebbles of the Blaini. Regarding the inclusion of Dagshai Sandstone Auden states[11]

"Dagshahi-like-sandstones occur as boulders in the Blaini boulder bed *which is without question pre-Tertiary and with fair certainty pre-Mesozoic, thereby proving* that there must be at least two series of sandstones of similar types, one pre-Mesozoic and the other Tertiary." This assumption of the occurrence of Dagshahi-like-sandstones in pre-Mesozoic series is unwarranted since no types are known. There is however no need to make any such assumption if the 'Blaini boulder bed' is divested of its stratigraphic significance.

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[9] *G. S. I.*, **21**, 136.
[10] *Ibid.*, **67**, 425.
[11] *Ibid.*, **67**, 440.

The position with respect to the age of the Himalayan Granites is still more interesting, if intriguing. Auden has described a small pebble of granite found in the 'Volcanic breccia' at Raitpur in Garhwal. Middlemiss places this 'Volcanic breccia' at the base of his 'Purple Slate' series which Auden correlates with his Mandhalis. According to Auden "the breccia at Raitpur lies abnormally above the Tal beds and is itself overlain by the 'Inner Schistose Series' with its capping of gneissic granite'.[12] Auden further writes in this connection.[13] "The Blaini" (with which Mandhalis are tentatively correlated) is now regarded as the same age as the Talchirs, which are Upper Carboniferous in age. It was considered by Sir Thomas Holland to be Purana but Pilgrim and West following Oldham correlate it with Talchirs. "No one has suggested an age younger than Upper Carboniferous." "It follows that the pebble of granite must be derived from a parent granite" of earlier than Upper Carboniferous age.

Petrologically, on the other hand, the granite boulder according to Auden, corresponds very closely with the granites of the Arwa valley which according to Griesbach and Hayden must be of Cretaceous or Tertiary age.[14]

From this it will be seen that taken as a stratigraphical unit the age of the boulder bed containing the granite pebble may be anything like Purana, pre-Carboniferous, Upper Carboniferous, Cretaceous or even Tertiary.

On the other hand the field evidence as noted by Auden clearly indicates that the breccia of Raitpur lies between the Tal Beds, below, and the Inner Schistose series with a granite capping, above it. It is obvious that the Raitpur breccia at this abnormal junction marks an important thrust plane and as such it is very easy to conceive of a pebble of the overlying granite rock getting enclosed in the breccia along the thrust.

Evidence of Surface Markings

Besides the nature of the boulders and of the associated clay the most important evidence which prompted the early investigators to favour glacial origin for the Blaini boulder bed was the nature of surface markings in the form of scratches or striations, accompanied by smoothening of the surface. No other agency was then known which could produce such markings. It is somewhat remarkable that the originator of the Glacial theory for these beds should have been more cautious and halting in assessing the value of these markings than some of the later authors who followed him. Oldham

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[12] *G. S. I.*, 66, Pt. 4, 461.
[13] *Ibid.*, 66, 462.
[14] *Ibid.*, 66, 464.

was aware of the extreme paucity of boulders in the Blaini bed with truly glacial markings while he also realised that similar markings could as well be produced by compressional movements. Describing the boulder bed of the type locality he wrote "No smoothed and striated boulders have been found as yet though one is occasionally met with showing striation resembling those produced by glaciers but the rock has invariably undergone much compression and disturbance at times accompanied by a distortion of the shape of the included fragments which might account either for the obliteration of distinctly glaciated surfaces or for the production of those scratches which have been observed. No certain conclusion can, consequently, be drawn from the occasional presence or general absence of striation....."[15]

The true position regarding surface markings on Blaini boulders could not have been presented in a clearer way. Oldham himself could not put in too much reliance on the evidence of surface markings such as those observed on the boulders, in support of his glacial theory for the Blaini bed. Had he been aware of extensive thrust movements in these regions it is possible he would have discarded the glacial interpretation of these surface markings.

Later writers, however, appear to be more enthusiastic than critical in accepting the glacial theory and have adhered to it. No doubt two boulders were discovered which were distinctly scratched and were described as glaciated boulders by Holland.[16] The markings as described do not appear to be an unequivocal evidence of glaciation.

Middlemiss describing the Hazara Basal conglomerate wrote "The pebbles show evidences of turning round in their matrix sheared slightly one over the other and arranged with their long axis at a high angle with their original plane of bedding."[17]

Here then is a very clear evidence of the tectonic nature of the 'Basal conglomerate' in which, also, must be sought the origin of any scratchings that may be seen on the boulders.

The surface markings, rare and ambiguous as they are, do not positively lead to a glacial origin in this case.

Field Relations

In its field relations the conglomerate band is very commonly underlain by Dogra or Simla Slates and is overlain by a thick series of quartzites

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[15] Oldham, *Manual of Geology of India*, p. 133.
[16] *Rec. G. S. I.*, 37, Pt. 1, 129–35.
[17] *Mem. G. S. I.*, 26, 230.

with an intervening bed of sandy shales, as we find in Hazara, Poonch, Simla region, etc.

Hazara Region.—In the Hazara region Wynne and Waagan had described the conglomerates as a breccia bed resting unconformably on the upturned edges of the slate series. The bed is composed of fragments of underlying slates and quartzites set in a fine purple sandy clay or shale. The pebbles are generally subangular but show no trace of striæ or scratches. Wynne and Waagan who have worked extensively both in Hazara and in Salt Range consider the Hazara boulder bed as of Cretaceous age. On the other hand, Oldham, as usual, considers this unfossiliferous boulder bed which is infra-Trias in position, as of glacial origin and compares it with the Salt Range boulder bed.

Middlemiss writing about Hazara Basal conglomerate bed as typically exposed in Sobruh Gulee, states[18] :—

"Here the conglomerate which is about 30′ thick is made up of fragments of nothing but slates and quartzites. No trace of gneissic rocks or of any highly crystalline schists is found embedded as pebbles in the conglomerate."

The same conglomerate band occurs beneath the quartzites in the Miankhaki stream and thus marks the thrust junction between the slates and the overlying quartzites.

Simla Hills.—If we look at the geological map of the Simla Hills by Pilgrim and West[19] we see the extensive distribution of the Blaini bed north of the Ashni-Giri rivers. The Krol belt, in the sense in which it is so far understood, is restricted to the south of these rivers and in this Krol Belt the development of the Blaini boulder bed is very minor and infrequent. If the Blaini boulder bed were a normal member of the Krol sequence as it has been regarded till now, it is curious why it should be so insignificant and infrequent in the Krol Belt in contrast to its abundant development in the north where the Krol sequence is altogether absent. This strongly suggests that the boulder bed is not a regular member of Krol sequence.

Again, north of the Ashni-Giri line the Blaini boulder bed is found occurring almost continuously at the junction of the Simla slates and the Jaunsar quartzites. It is recognised by Pilgrim and West that in this region the Jaunsars have thrusted over the Simlas. The boulder bed

[18] *Mem. G.S. I.*, **26**, 230.
[19] *Ibid.*, **53**, Pl. 1.

consistently follows this thrust plane which is the Jaunsar Thrust. The presence of boulders of slates and quartzites in this bed proves beyond doubt that the boulder bed is only a cemented thrust breccia formed by the movement of Jaunsar quartzites over the Simla slates.

Thus in most cases the field evidence shows that this conglomerate bed occurs between two formations of dissimilar ages, the older one generally resting over the younger one, thus marking a plane of over-thrust. From this discussion of occurrences in widely separated areas the following features stand out prominent.

1. That the conglomerate 'bed' in the outer Himalayas is commonly found over the slates of Simla-Dogra-Hazara type and is overlain by quartzites of the Jaunsar type with or without the intervening layers of shales and limestones.

2. That the 'bed' is composed of fragments of the rocks with which it is associated both below and above. The fragments are set in a matrix of similar rocks in a more comminuted form. Besides the pebbles of Jaunsar quartzites and Simla slates the 'Blaini' bed in certain regions also contains pebbles of rock types like those of Infra Krols, Krols and even granites, and sandstones which are known to be of younger ages.

3. That there are several conglomerate bands which occur at the various thrust and over-thrust junctions.

4. That the pebbles and boulders show marks of irregular scratching and faceting and evidences of shearing, rolling and turning round in the matrix.

The first three features clearly indicate the provenance of the pebble meterial from the adjoining rocks both below and above, whereas the fourth factor obviously indicates movement of one rock formation over another leading to crushing and dragging of fragments *in situ*. These features can be explained only on the tectonic origin of the conglomerate band and not by glaciation or normal sedimentaiton. This is all the more plausible since field distribution appears to show that the 'Blaini conglomerate' is not a regular member of Krol or any other sequence.

We are perfectly aware that large-scale horizontal movements connected with Himalayan Orogenesis have actually taken place before or during the middle Tertiary period. Auden, for example, estimates the translation along the Garhwal Thrust alone to be over fifty miles. And a number of such thrusts are already recognised. It is therefore quite possible that the so-called Blaini conglomerate bed is just a crush breccia formed during one or more of such thrust movements.

If this conclusion is accepted numerous apparent anomalies would be easily resolved.

We can easily explain the occurence in this conglomerate of boulders of overlying rocks and also those of much younger rock types, *e.g.*, Infra-Krols, Krols, etc., we can also account for the almost complete absence of meso-metamorphic rocks among these boulders. Further there is no need of invoking the presence of a pre-Permian sandstone formation to account for pebbles of Dagshai like sandstone, nor need we divide the granites into Tertiary and pre-Permian, simply because granitic pebbles happen to occur in the conglomerate. Again, we need not postulate glacial conditions in Permian times to explain the scratching and faceting of boulders.

Another Mode of Formation

It must however be added here that not all boulder beds of the Himalayas need be of the thrust breccia type, for, besides this particular type, another mode of formation can be visualised for some bands which do not show evidences of crushing. We can imagine a stage when after the first phases of the Himalayan upheaval the rock formations were thrown into sharp anticlines and synclines somewhat of an asymmetrical nature. This gave rise to consequent longitudinal river system. Owing to the young nature of the mountain system and continuous diastrophic movements the rocks were being rapidly broken on a large scale and transported along the longitudinal valleys. These got mixed up with the fine detritus of the neighbouring rocks and filled up the valleys. When the next upheaval took place the rock formations were more closely folded in and this loose detrital material got entrapped within the folds of older rock formations as a compact bed. This mode of origin would easily account for a large number of conglomerate bands in one and the same formation as well as in many other formations of widely different ages. This would also account for the rounded boulders of different sizes which occur abundantly in the ' Blaini ' conglomerate as is remarkably seen in the Kewal Khala (Simla Hills).[20]

Conclusion

From a closer study of the lithology and field relations of the 'Blaini Boulder Bed' in different areas in the Himalayas it seems clear that the evidences on which the stratigraphical importance of the bed as a glacial formation of Permo-Carboniferous age was based are liable to other and more convincing interpretation which divests it of that importance.

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[20] Rode, K. P., *Q. J. G. M. M. Soc. India*, 1942, 14, No. 2, 65–73.

The variety in size and form of the boulders as also their occasional surface markings which so far had been interpreted as denoting definite glacial action are all to be expected in rock fragments formed during *Nappe* movements along thrusts. Some of these features could also be attributed to valley detritus formed during folding movements.

The lithological study of the included boulders indicates their derivation not only from the rocks below the boulder band but also from the rocks above it.

The field position of the boulder 'bed' is also not definite; the 'bed' occurs variously at the junction of widely different rock formations the Jutoghs, Jaunsars, Simlas, Infra-Krols, Krols, etc., and more particularly at those junctions where an older rock formation occurs superposed over a younger one with an abnormal contact.

These evidences are definitely against the glacial origin and lead one to conclude that the boulder formation is either a thrust breccia or a valley detritus formed during tectonic phases of Himalayan upheaval.

In this continuation it may be pointed out that even the Salt Range Boulder Bed offers evidences of thrust movements[21] and of the derivation of some fossiliferous boulders from the overlying rocks.

It may at this stage be questioned whether any truly glacial beds of Permo-Carboniferous or any pre-Tertiary age occur at all within the Himalayan region. The possibility is not ruled out but their existance must be proved on better evidences.

It is further not unlikely that many of the so-called Permo-Carboniferous boulder beds of other tectonically folded regions may ultimately turn out to be only crush conglomerates and may not have anything to do with Permian Glaciation. Permian Glaciation in such areas would need better proof.

Before closing this article the author wishes to state that the views expressed here are primarily based on personal observations made in the Sirmoor and Solon Hills, and on the consideration of evidences recorded from other regions. The conclusions arrived at, during this limited study, are widely at variance with the long accepted notions arrived at over 50 years back, but, since the problem of the Blaini Boulder Bed has assumed fundamental importance in Himalayan geology, it is only proper that a

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[21] *Rec. G. S. I.*, 62, 416.

critical review is made every now and then of all the available field and laboratory evidences to help us in properly understanding the nature and mode of origin of this interesting rock formation.

The aim of this contribution is to put forward, as a suggestion, another interpretation of the evidence which to the author appears more convincing and capable of a more general application, not only in the Himalayas but also in other tectonic mountains.

In the end the author wishes to express his indebtedness to the Sirmoor Darbar for the facilities which enabled him to make these observations in the field. The author had the pleasure of the company of Messrs. Muktinath Gupta and Achyuta Rao during these investigations. He is also thankful to Prof. L. Rama Rau for critically going through the manuscript and for making helpful suggestions.

THE EFFECT OF HYDROGEN IONS AND TONIC CONTRACTION ON THE VISCOSITY OF UNSTRIATED MUSCLE

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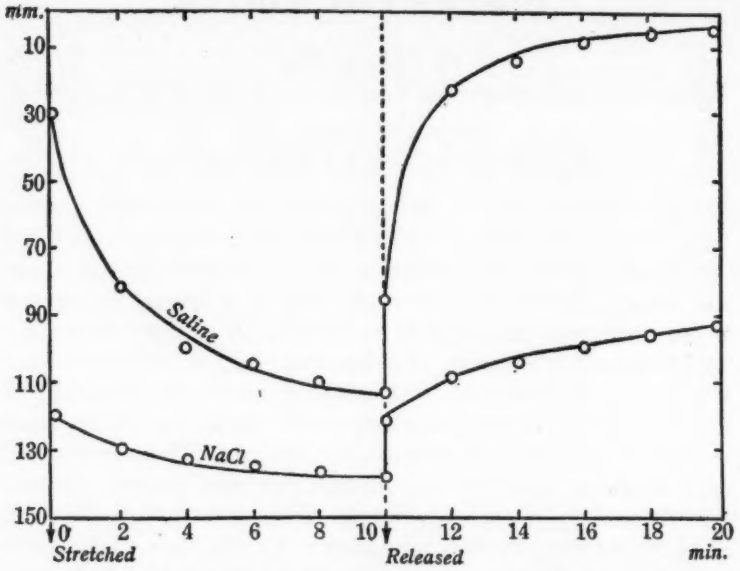
Compared to striated muscle, the movements of plain muscle are sluggish; this sluggishness has been ascribed to increased viscosity of the latter.[1] The sluggishness particularly affects the relaxation and it has been calculated that the oxygen consumption corresponding to a tetanus in plain muscle would not necessarily be enough to be detected by oridnary methods, owing to this characteristic slowness of relaxation, due to increased viscosity.[2] The sluggishness of movement of plain muscle can be experimentally varied ; it is increased by all substances causing tonic contraction and by decrease of temperature;[3, 4] relaxation is particularly affected.[4] The viscosity of Mytilus plain muscle is higher in a contraction produced by direct current than in that produced by alternating current; the contraction produced by the former is characterised by slow relaxation.[5] During slow relaxation there is no increase in the oxygen consumption of plain muscle.[3] Life is not necessary for this slow relaxation.[6] Plain muscle becomes more (economical) if treated with carbon dioxide ; this increase in "economy" is due to retardation of relaxation.[7] It would be interesting to know the effect of hydrogenions on the viscosity of plain muscle. Plain muscle becomes more economical with exercise[7]; this decreases the rate of relaxation and oxygen consumption is not increased.[3] The viscosity of striated muscle is increased by fatigue.[8] Tone increases and adrenaline decreases the viscosity of the dog retractor penis.[9]

Methods

Stretch and release curves[3,4,9] of the anterior retractor of the byssus of *Mytilus edulis* were recorded. Two methods were used to determine the viscosity. According to Winton,[9] the time-extension curves of unstriated muscle are compounded of an exponential phase, resembling those of striated muscle and a linear phase. The equation of these curves is of the form $At+B\ (1-e^{-kt})$. If from these curves the linear phase is subtracted, one will be left in plain muscle with something akin to striated muscle, the equation for extension of which according to Bouckaert, Capellan,

and De Blende[10] is log $(C/K_1 - A\nu) = -K_1 t/K_2\eta + \log C/K_1$ where K_1 is a factor proportional to the modulus of elasticity, $K_2\eta$ is the coefficient of inner friction or viscosity, C is the constant force of the undamped



spring, and $A\nu$ is the viscous extension. After subtracting the linear phase from the time extension curves, $K_2\eta$ and K_1 were determined from the remaining exponential phase by means of the above equation.[10] The gradient of the linear phase was measured just after the exponential phase merged into it, *i.e.*, in the period from 10 to 20 minutes of the time extension curve.

The second method was to compare the gradients of the linear phase. The linear extension of the muscle will be directly proportional to the force and inversely proportional to viscosity. In plain muscle the extending force is opposed by the contractile force of tone, so that the rate of extension will be proportional to (mg-T)/K, where mg = extending force, T = tone, and *k* the coefficient of viscosity ; the rate of shortening will be proportional to T/K. Any substance that increases tone will diminish the rate of extension, and increase that of shortening, as has been found experimentally.[4]

If a substance does not cause contraction, then (mg-T) remains constant, and the effect of viscosity is determined directly by comparing the gradients of the extension curves.

The effect of pH was determined by bubbling mixtures of air or oxygen and carbon dioxide through sea water, or by adding acetic or lactic acids

to the sea water; the latter was not buffered, as buffers such as borax caused contraction. The Mytilus saline was buffered with phosphate or acetate. The muscle was immersed in the control solution before and after immersion in the experimental solution (the time of immersion being 2 hours); the mean of the two results was taken for the value in the control solution.

The effect of contraction was determined by immersing in the potassium rich saline (0.1 M KCl) for two hours and in other substances, such as caffeine, adrenaline, the muscle was immersed for fifteen minutes ; the contraction produced by potassium lasts several hours. Immersion for fifteen minutes in potassium solution gave identical results.

Effect of ph on Viscosity

TABLE I *a*

pH	No. of Expt.	Viscosity
8·3	..	100
7·8	1	64
	2	18
	3	77
6·6	4	333
	5	125
5·2	6	245
	7	235
	8	123
5	9	500

TABLE I *b*

No. of Expt.	pH	$K_2\eta \times 10^3$	K
1	8·3	30	43
	7·8	18	52
	7	22	60
2	8·3	52	74
	7·8	48	74
	6·5	53	80
3	7·8	25	83
	5	31	141
4	7·8	15	76
	5	30	266
5	7·8	18	52
	4·4	62	223
6	7·8	27	47
	4·4	45	108

Results

The effect of pH (Table I *a*, *b*). Change in pH from 8·4 to 5 does not cause contraction of the muscle, so that its effect can be determined by comparing the gradients of the linear phase. The pH of sea water was 8·3 and the gradient of extension in this was taken as unity. The results are shown in Table I *a*. The numbers represent

$$\frac{\text{gradient at pH 8·3}}{\text{gradient at the experimental pH}} \times 100.$$

The viscosity is minimum at pH 7·8. The excitability of the muscle is maximum at this pH; this inverse relation between excitability and viscosity is interesting. All substances that increase the viscosity, diminish the excitability and the mechanical response.

pH 4·4 causes contraction of the muscle. It increases tone and viscosity[11] (Table II). pH 3·8 causes irreversible changes.

TABLE II

Effect of Tonic Contraction on viscosity

No. of Expt.	Solution	$K_2\eta \times 10^3$	K_1	Result
1	Sea water	17	51	
	0·1 M KCl	296	440	Contraction
	0·5 M KCl	0·296	19	Relaxation
2	Mytilus saline pH 7·8	14	34	
	0·1 M KCl pH 7·8	32	66	Contraction
	0·1 M KCl pH 7	18	46	Relaxation
	0·1 M KCl pH 6·5	12	46	Do.
3	Mytilus saline pH 5	31	140	
	0·M KCl	36	152	Contraction
4	Mytilus saline	18	66	
	0·1 M KCl	23	102	Do.
5	Sea water	53	89	
	0·1 M KCl	116	221	Do.
6	Mytilus saline	4·1	53	
	Ca-free saline	34	148	Do.
7	Mytilus saline	9·1	43	
	Ca-free saline	18	62	Do.
8	Mytilus saline	6·8	82	
	0·01 M $BaCl_2$	7·2	82	Do.
9	Mytilus saline	10	40	
	0·5 M NaBr	14	52	Do.
	0·5 M $NaNO_3$	17	104	Do.
10	Mytilus saline	2	78	
	Caffeine 1 in 1000	10	332	Do.
11	Mytilus saline	4·5	39	
	Isotonic glucose	23	110	Do.
12	Mytilus saline	3·9	55	
	Adrenaline 1 in 10^5	1·0	19	Relaxation
13	Sea water	45	118	
	0·08 M Mg	28	78	Do.
14	Sea water 15° C.	4·5	119	
	Do. 25° C.	3·7	83	
	Do. 35° C.	2·9	46	
15	Sea water, freshly disected muscle ..	11	409	
	After frequent stimulation with alternating current 10 V–10 Sec. ..	2·8	44	
	After frequent stimulation with direct current 8 V–10 Sec.	4	70	

In solution of other ions, the sodium of the saline is replaced by equivalent amount of these ions. To sea water isotonic solutions of these ions are added with necessary calcium, magnesium or potassium, as the case may be, so that the concentration of these latter ions is kept constant.

Release curves were also recorded ; they showed decrease in the rate of change of length with change of pH on either side of 8·3.

The effect of tonic contraction (Table II). All substances that cause tonic contraction increase $K_2\eta$ and K_1. These results are similar to those on striated muscle;[12] in unstriated muscle, the increase in value of K_1 with contraction is less. This is probably due to the fact, that isolated unstriated muscle is already partially contracted to begin with; if fully relaxed and fully contracted muscle is compared the change is greater (Expt.1). 0·1 M KCI causes contraction, and 0·5 M KCI causes almost complete relaxation; in contracted muscle the change in viscosity is 1,000 times greater. Plain muscle is thus capable of much greater changes in viscosity. The average value of $K_2\eta$ is 27×10^3. If the average length of the muscle be taken as 2 cm. and volume 0·15 cc., for unit length and section this reduces to 72×10^4. For striated muscle the value is about $1{\cdot}2 \times 10^{3,10}$ so that unstriated muscle is about 100 to 1,000 times more viscous than striated muscle and its movements are more than 100 times slower.[8]

In 6 experiments (2 with pH 4·4, 1 with Ca-free saline, and 3 with 0·1 M KCI) release curves were recorded with similar results, but the value of viscosity was found to be 40 to 80 p.c. of that found in stretch curves. In 0·1 M KCI the value of K_1 was however increased, so that these muscles were contracting; Mytilus muscle contracts on release.[15] Thus the viscosity of a *contracting* muscle decreases, while that of a *contracted* muscle, increases. This is in agreement with results of Winton,[5] who found that the viscosity decreases during contraction produced by alternating current. Further, in Mytilus muscle it has been found, that when it relaxes slowly in 0·07 M $BaCI_2$ in Mytilus saline, before it contracts again the rate of relaxation suddenly increases, so that the viscosity decreases.[17]

During contraction two processes occur, one that produces tension, and the other that reduces viscosity.[3] In the above experiment the two processes are disassociated, and the process producing reduction of viscosity precedes that producing contraction. When the muscle is stimulated with alternating current, the former process outlasts the latter, so that the viscosity is decreased after stimulation (5; experiment 15, Table II).

The reduction in viscosity during contraction is to facilitate movement, and in plain muscle the rate of relaxation may be greatly decreased, while the rate of contraction remains comparatively unaffected.[6,7] This decrease in viscosity appears to be due to liberation of calcium (17 ; expts. 6, 7, Table II).

This mechanism does not seem to be present in isolated skeletal muscle wherein it is not necessary owing to the absence of tone, as the latter is attended with increased viscosity. Tone decreases just after stimulation with potassium, acctylcholine, alternating current in dog stomach, dog retractor penis, pig stomach, frog stomach and after alternating current in Mytilus muscle,[15] the process of reduction of tone and viscosity having outlasted the process producing contraction. In plain muscle alternating current is antagonistic to tone.[15, 19, 20] In plain muscle it is probable that the factor that increases viscosity of skeletal muscle during contraction, occurs, but the second process not present in the latter, neutralises this; the contradictory results of Winton on one hand and those of Gasser and Hill on the other, are explained.

Discussion

These results are derived from an empirical equation, but it is unwise to lay too much stress on comparison between plain muscle and any mechanical model.[13] The results are, however, of comparative value and the theoretical interpretation is that plain muscle stretches like striated muscle producing the exponential phase and tone yields before the extending force producing the linear phase. The rate of extension is influenced by viscosity. The results are in agreement with previous views[3, 4, 6, 11, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23] and with those of other workers using quite different methods.

The slow relaxation of unstriated muscle is attended by increased viscosity; there is absence of heat production, potential, oxygen consumption and even life may be absent.

Summary and Conclusions

(1) Plain muscle is capable of great changes in viscosity. The viscosity of plain muscle is about 100 to 1,000 times that of striated muscle and its movements correspondingly slower.

(2) The viscosity of plain muscle increases as a result of tonic contraction, but is decreased during active contraction.

(3) Hydrogen ions increase the viscosity; the optimum pH is 7·8, change on either side increasing the viscosity. The excitability is maximum at this pH.

(4) Substances that decrease the rate of relaxation, increase the viscosity; plain muscle is thus able to keep up tension without expenditure of energy. During active contraction, viscosity decreases to facilitate movement.

APPENDIX

Tonus with low viscosity

In the above paper has been described tonic contraction attended with high viscosity. Singh (1942 *b*) has described two kinds of tone, one with low and the other with high viscosity. The tone with low viscosity is found in guinea pig uterus, as is evident from the figure. The upper curves are in mammalian saline, the lower in isotonic sodium chloride. The curves were complicated by spontaneous contractions and so the release curves are not of much significance; the stretch curves, however, show low viscosity.

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ISOTONIC EXTENSION OF UNSTRIATED MUSCLE

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Isotonic extension of unstriated muscle has been described by Jordan (1929); Winton (1930, 1937); Singh (1938, 1940, 1942 *a*, *b*). Unstriated muscle when stretched gives three kinds of curves. In the first kind there is a continuous curvature throughout and there is no linear phase (Fig. 1). In the second there is a point of inflexion with the curvature now in the opposite direction, followed by another point of inflexion with the curvature returning to the original direction (Fig. 2). The third curve is intermediate between the two, there being a linear phase (Fig. 3).

In this paper the curve with the linear phase is taken as the standard curve and variations from it are discussed.

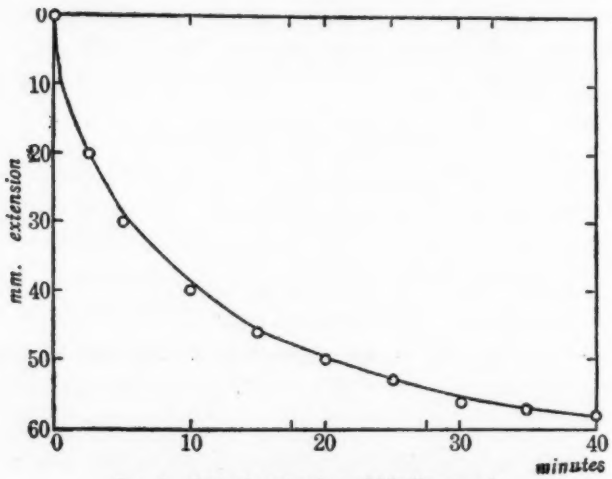

Fig. 1. Isotonic extension of Mytilus muscle
Magnification 7 times, load 19 grams

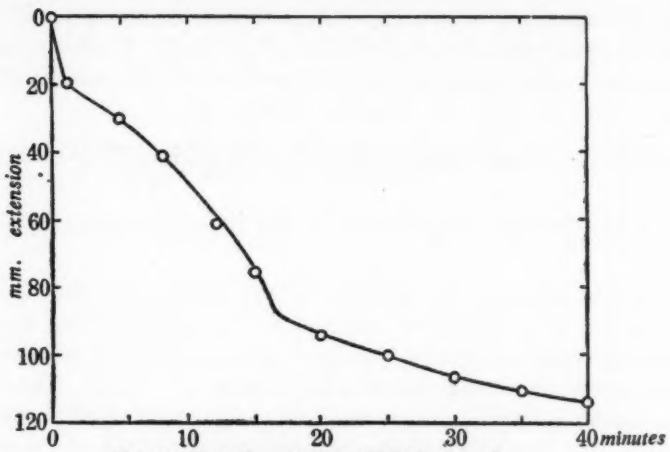

FIG. 2. Isotonic extension of Mytilus muscle

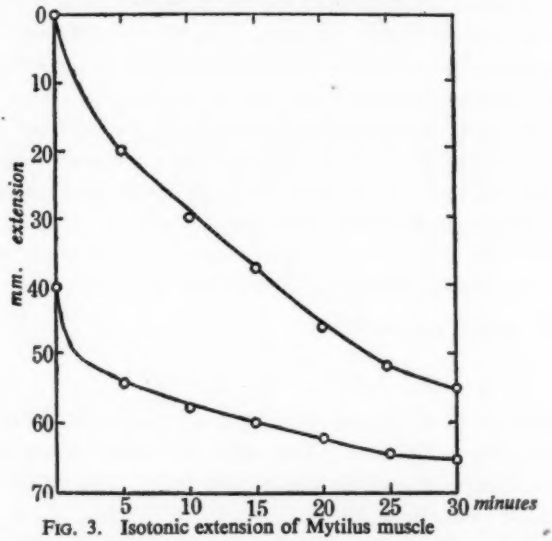

FIG. 3. Isotonic extension of Mytilus muscle

Two equations fit the time extension curves with the linear phase (Singh, 1942 *a*, *b*).

$$x = \frac{c}{p}\,(1 - e^{-\frac{pt}{k}}) + At, \qquad (1)$$

where x = extension, t = time, c = constant force of the undamped spring, p = restoring force proportionate to the modulus of elasticity, k = coefficient of inner friction or viscosity, A is a constant.

$$x = m\left(\frac{v^{\circ}}{k} - \frac{mg - T}{k^2}\right)(1 - e^{-\frac{kt}{m}}) + \frac{mg - T}{k} \cdot t, \qquad (2)$$

where m = extending weight, g = force of gravitation, v = initial velocity of the damped phase, k = coefficient of viscosity, T = force of tone. In this equation v, the initial velocity, like the final velocity, will be proportional to $mg - T/k$, so that the equation reduces to

$$\frac{m(mg-T)}{k^2}(c-1)(1-e^{-\frac{kt}{m}}) + \frac{mg-T}{k} \cdot t, \tag{3}$$

where c is a constant proportional to the impulse received by the damped phase.

The first equation fits majority of the curves, but has no theoretical basis, so that it is difficult to explain the variations of the linear phase. The second equation explains the linear phase in majority of the curves, but its exponential factor fits only a small number of curves. The exponential factor increases with viscosity, as is found in some experiments. In one experiment, a diminution of the exponential factor with increase in weight has been recorded, as demanded by the equation ; this is probably due to the response to stretch (Singh, 1938 *b*). The second equation will therefore be used to explain the variations in the linear phase of the time extension curves.

Effect of adaptation.—When to the muscle is added a substance that causes contraction, to which it subsequently adapts, then the curve is of the kind shown in Fig. 2. The increase in the velocity of extension prior to the exponential diminution is thus due to adaptation. The equation that represents these curves is of the form

$$x = At + B(1 - e^{-\frac{kt}{m}}) - ct + bt^2, \tag{4}$$

where c, b and k are constants.

$$x = At + B(1 - e^{-\frac{kt}{m}}) - ct + de^{kt}. \tag{5}$$

Adaptation is a process by means of which the force causing contraction, diminishes with time. The simplest assumptions are that the force diminishes linearly or exponentially with time. The equation for the motion of the system will then be

$$m\frac{d^2x}{dt^2} + k\frac{dx}{dt} mg - T - (F - bt) \tag{6}$$

$$m\frac{d^2x}{dt^2} + k\frac{dx}{dt} = mg - T - (F - he^{kt}), \tag{7}$$

where F is the force of contraction and b is the coefficient of adaptation, and h a constant.

$$m\frac{d^2x}{dt^2} + k\frac{dx}{dt} = mg - T - Fe^{-kt}. \tag{8}$$

When the equations 6 and 7 are integrated, the solutions are similar to equations 4 and 5 respectively, so that the assumption about adaptation is probably correct. The solutions of the equations 6, 7 and 8 respectively are

$$x = \frac{m}{k}\left(v^0 - \frac{mg - T - F}{k} + \frac{bm}{k^2}\right)\left(1 - e^{-\frac{kt}{m}}\right) - \frac{m}{k}\left(\frac{b}{k^2} - \frac{mg - T - F}{k}\right)t + \frac{k}{2b}\cdot t^2 \qquad (9)$$

$$x = \frac{m}{k}\left(v^0 - \frac{mg - T - F}{k} - \frac{1}{mb + k}\right)\left(1 - e^{-\frac{kt}{m}}\right) + \frac{mg - T - F}{k}\cdot t - \frac{h}{b(mb + k)}\left(1 - e^{bt}\right) \qquad (10)$$

$$x = \frac{m}{k}\left(v^0 - \frac{mg - T}{k} + \frac{F}{k - mb}\right)\left(1 - e^{-\frac{kt}{m}}\right) + \frac{F}{b(k - mb)}\left(1 - e^{-bt}\right) + \frac{mg - T}{k}\cdot t \qquad (11)$$

In equations 6 and 7, the value of x is only valid till $F = at$, or $F = he^{bt}$. But if the substance produces adaptation to tone also, such as happens with adrenaline, veratrine, then the equation is valid for greater values of F.

Effect of initial length.—When the muscle is stimulated with potassium, with increase in initial length, the tension may increase linearly for a considerable period, follow a parabolic course, or diminish exponentially (Singh, 1938 *b*). The equations for extension will therefore be

$$m\frac{d^2x}{dt^2} + k\frac{dx}{dt} + Fx = mg \qquad (12)$$

$$m\frac{d^2x}{dt^2} + k\frac{dx}{dt} = mg - Fe^{-rx}, \qquad (13)$$

where r is a constant

$$m\frac{d^2x}{dt^2} + k\frac{dx}{dt} = mg - ax + bx^2. \qquad (14)$$

The solution of equation 12 is

$$x = \frac{1}{a - b}\left\{v^0\left(e^{-bt} - e^{-at}\right) + \frac{amg}{F}\left(1 - e^{-bt}\right) - \frac{bmg}{F}\left(1 - e^{-at}\right), \qquad (15)\right.$$

where $a = \frac{k}{2m} + \sqrt{\frac{k^2}{4m} - \frac{F}{m}}$, $b = \frac{k}{2m} - \sqrt{\frac{k^2}{4m} - \frac{F}{m}}$.

The damping is such that the motion is aperiodic. Fx acts like the restoring force; if the latter is not neglected then the solution will be similar.

There will be a continuous curvature in the time extension curves, as in Fig. 1.

Effect of viscosity.—If the viscosity decreases then the linear velocity will be reached later than when the viscosity is high, as in Fig. 4. Adaptation

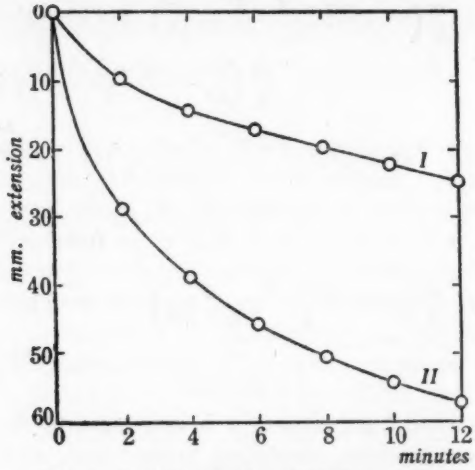

FIG. 4. Isotonic extension of Mytilus muscle
Curve 1, in Mytilus saline ; Curve 2, effect of 1 in 10^5 adrenaline

will reduce the viscosity, as well as change in length; change in viscosity with change in length is also shown in striated muscle (Bouckaert, Capellan and de Blende, 1935). The equations will be

$$m\frac{d^2x}{dt^2}+(p-kt)\frac{dx}{dt}=mg-\mathrm{T}-(\mathrm{F}-at) \tag{16}$$

$$m\frac{d^2x}{dt^2}\pm ax\frac{dx}{dt}=mg-\mathrm{T}. \tag{17}$$

Effect of stretch.—This will oppose the extending force, and may even temporarily exceed it, but the muscle soon adapts. The equation will be of the form

$$m\frac{d^2x}{dt^2}+k\frac{dx}{dt}=mg-\mathrm{T}-(\mathrm{F}-bt) \text{ or } =mg-\mathrm{T}-\mathrm{F}e^{-kt}. \tag{18}$$

Effect of spontaneous contractions.—The stretch curves of frog stomach are complicated by spontaneous contractions. These can be represented by a Fourier's series. The simplest rhythmic spontaneous contractions of plain muscle are represented by a sine curve, the equation being of the form $a+b\sin ct$. The spontaneous contractions of the guinea pig uterus are

more complicated and can be approximately represented by a limited number of the terms of the series

$$2\,[\sin t - \tfrac{1}{2}\sin 2t + \tfrac{1}{3}\sin 3t - \tfrac{1}{4}\sin 4t + \tfrac{1}{5}\sin 5t \ldots .] \qquad (19)$$

$$a + \sin t + \tfrac{1}{3}\sin 3t + \tfrac{1}{5}\sin 5t \ldots . \qquad (20)$$

The force causing extension would be periodic and the equation of the extension curve would be of the form

$$At + B\,(1 - e^{-kt}) - \left(a \sin \frac{\pi}{c}\, t + a_2 \sin \frac{\pi}{c} 2t \ldots .\right) \qquad (21)$$

the differential equation being

$$m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - T - b\,(a_1 \sin t + a_2 \sin 2t \ldots .). \qquad (22)$$

Crossing of curves.—When time extension curves cross each other (Fig. 5), then it is evident that two factors in the muscle have been oppositely affected;

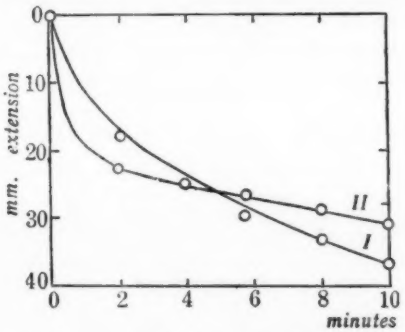

FIG. 5. Isotonic extension of Mytilus muscle
Curve 1, in 0·5 M $NaNO_3$; Curve 2, in 0·5 M NaI

the exponential and linear factors, if oppositely affected will produce such a result.

Partial contraction of muscle.—The question arises as to how the partial contraction of plain muscle is affected. Is it due to contraction of a partial number of fibres, or is it due to contraction of portions of fibres, or does it affect the whole fibre? Whatever happens it appears that the remaining uncontracted element is thereby strained if the length is fixed. This is seen from Fig. 6. The successive spontaneous contractions increase in magnitude, corresponding to increase in tension with the initial length. The contracted and non-contracted elements will have different viscosity producing two points of discontinuity instead of one, one at the junction of the undamped and the damped phases, and the other at the junction of phases of lesser and

greater viscosities (Fig. 7). The undamped phase may be regarded as damped by very low viscosity.

Discussion

During extension of plain muscle the following variables are involved : (1) tone, (2) viscosity, (3) extending force, (4) tonic contraction, (5) adaptation, (6) change of contraction with length, (7) change of viscosity with length, (8) change of viscosity with time, (9) stretch response. But most of these factors can be eliminated and so the analysis simplified. By prolonged soaking adaptation can be eliminated. Substances can be used to which adaptation is very slow. Thus Mytilus muscle adapts to 0·1 M KCl in about 16 hours ; it adapts to barium extremely slowly. Effect of length can be eliminated if partial extension only is taken into account (Singh, 1942 *a*, *b*), or solutions can be used in which length has no effect on tension. The linear phase should thus be studied just after the exponential phase emerges into it (Singh, 1942 *b*). Attention is drawn to other papers on the subject (Singh, 1938 *a*, *b*, *c*, *d*, *e*, *f*; 1939 *a*, *b*; 1940; 1942 *a*, *b*, *c* ; Rao and Singh, 1940).

Summary

There are many variables involved in the extension of plain muscle. These are (1) tone, (2) viscosity, (3) extending force, (4) tonic contraction, (5) adaptation, (6) change of contraction with length, (7) change of viscosity with length, (8) change of viscosity with time, (9) stretch, (10) restoring force.

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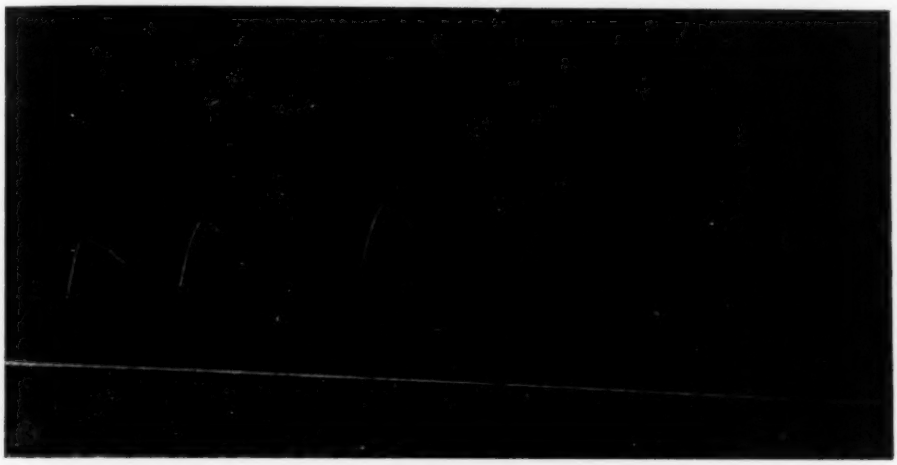

FIG. 6

Spontaneous contractions in Mytilus saline

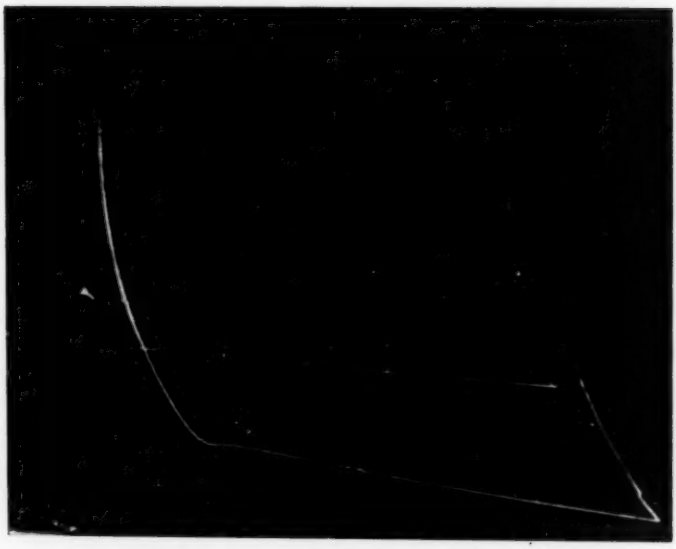

FIG. 7

Isotonic extension of Mytilus muscle in 0·5 M KCl

BIOLOGY OF A NEW ICHNEUMONID PARASITE OF THE AMARANTHUS STEM WEEVIL OF SOUTH INDIA

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(Communicated by Rao Bahadur V. Ramanatha Ayyar, L.Ag., F.A.Sc.)

Introduction

A study of the natural enemies of the Amaranthus stem-boring weevil *Hypolixus truncatulus* B. in the environs of Coimbatore has been in progress since 1935. During this period considerable quantities of material consisting of the weevil stages and their parasites have been handled. Some attention has been therefore devoted to the study of the biology of the weevil and also that of the rather formidable array of its parasites. An account of some of these was presented before the Indian Science Congress, Calcutta (1938). The investigation was however far from exhaustive since it has not been possible to bestow undivided attention to same. Recent studies on the same subject have revealed some new and interesting species of parasites which have not been recorded hitherto from India. One such species of parasite forms the subject of this short paper.

The Parasite

The species in question is an ichneumonid parasite belonging to the genus Xoridescopus. The genus Xoridescopus was erected in 1907 by Cameron to include the new species *X. annulicornis* from Borneo.[1] An extensive search of all the available literature has failed to reveal any other record of this genus. Further, this appears to be the only species so far known or recorded. The parasite in question is apparently very divergent from the only known species. It is quite possible therefore that this species occurring in South India is new to science. A detailed description of the same will be attempted as soon as the concerned literature becomes available. Meanwhile, the following description will suffice to distinguish the parasite. The species is a primary ectophagous parasite of the grubs of the common stem-boring weevil *Hypolixus truncatulus* B. of South India. It was for the first time reared from the host in November 1940. Numerous recoveries of the same from the same host in Coimbatore and surroundings have been made since. Since the parasite

[1] *J. Straits Br. R. As. Soc.*, No. 48, 18 and 19.

has not been previously recorded from India and since it is of some importance as attacking this host, a description of the morphology and biology, particularly of its immature stages, is presented in the following paragraphs. A detailed study of the species in regard to the development of cephalic skeleton and skin armature has been attempted since these form the main distinguishing characters of the larva.

Host Records and Distribution

Little information is available concerning other hosts of the parasite. From observations so far made, the primary host appears to be the grubs of *Hypolixus truncatulus*, the Amaranthus stem weevil. There is a single specimen in Coimbatore collections reared from the grubs of the weevil *Alcides affiber* from *Hibiscus cannabinus* stems. Numerous laboratory trials have been made in order to obtain an idea regarding possible alternate hosts of the species. The parasite oviposited on a few and developed into adults successfully. Among these, the grubs of *Alcides* spp. boring in stems of Daincha, Agathi, Bhindi, *Hibiscus ficulneus* were occasionally oviposited upon. Successful development has however taken place only in trials with Daincha, *H. ficulneus* and *H. cannabinus*. The egg-laying capacity was in all these cases observed to be considerably diminished. Never more than a maximum of 5 eggs was found laid per female. Besides, the pupal period was in majority of cases appreciably prolonged. In one instance it exceeded even one month.

The Adult

The adult (Fig. 1) is a handsome shining bluish black wasp-like insect with conspicuous greyish white markings on head and body. The female varies very much in size averaging about 14 mm. in length (excluding ovipositor). The male is considerably smaller and averages about 8 mm. in length. The head is black, closely punctate above and somewhat rectangular in shape, with the face, clypeus and orbits greyish white. The eyes are fairly large and dark brown. The antennæ are long but shorter than body and hardly attenuate anteriorly having about 21 flagellar joints in the female and about 25 in male. These latter are in colour black except for a pale band covering the third quarter of their length. The thorax is black with pale markings on neck and shoulders and a pale pronotal band. Mesonotum has a white central dark mark and the scutellum is pale white with a central dark mark. Metathorax has a white band over the basal area, a white patch on either side of middle area and a large white patch on post area. The wings are hyaline and large with an expanse of about 17 mm. across. The legs are reddish except at the tarsus. The abdomen is black with the segments edged with pale grey bands posteriorly. The ovipositor is

conspicuous and is about three quarters of the length of the abdomen (Fig. 2).

The male is easily distinguished from the female by the absence of ovipositor, by the larger number of flagellar joints and by their distinctly smaller size.

Habits of the Adult

The adults are fairly active and display a restless temperament particularly the females. They are positively phototropic as seen from their behaviour in rearing cages. These make incessant attempts to move and escape towards lighted portions of cages or laboratory. The matings were occasional and generally commenced soon after emergence. The mating preliminaries are brief and simple and the performance itself was of slight duration. Except for the excitement of the male and the vibration of antennæ, the process of coition may be described as quick and normal and did not exceed a minute in duration.

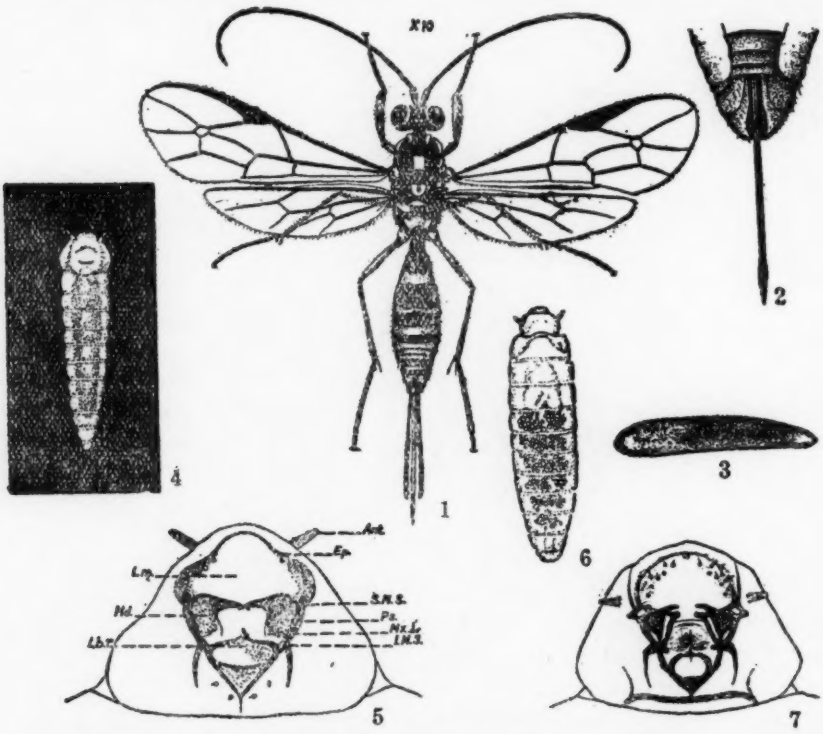
Oviposition

The process of oviposition has been watched several times in cages in the laboratory. The cages provided were simple and consisted of large sized tubes 6″ × 2″. Active non-parasitised grubs were dissected out from the host plant and suitable stages were lodged in artificial cells scooped out in small bits of fresh amaranthus stems and introduced in these cages with a mated female. The preoviposition period ranged from 3 to 5 days averaging 4 days for 12 individuals. This period was the same for both mated and unmated females. During this period the parasite rarely paid any attention to the loaded stems provided in the cages. A free crawling naked grub never excited her curiosity and was never ovipositted upon. At the end of the preoviposition period, the female took an active interest on the stems supplied and moved about the stem in her search for host grubs. She is guided in the location of the grub apparently by the vibrations caused by the movements of the grubs within the stem. A dead, diseased or inactive grub was never seen oviposited upon. After locating a healthy active grub, the abdomen is lowered and bent downwards almost at right angles to the rest of the body and a quick deep thrust into the stem is effected by the long ovipositor. After thus stabbing and paralysing the host, an egg is laid on it, the entire process occupying about two minutes at the maximum but averaging about a minute. The stages preferred for oviposition were the late third instar grubs and the fourth instar. Occasionally late second instar and mature grubs were accepted. Ordinarily a single egg is laid on any part of the paralysed host. Rarely two eggs were deposited on a single host. The maximum number laid by a single female per day never exceeded three eggs. The greatest number seen laid on

a single host was six in the course of two days. The total egg-laying capacity of a female varied from 5 to 34 eggs averaging 16 in twelve cases. The maximum egg-laying period noted was 61 days. The post-oviposition period averaged two days for a dozen cases under observation.

Description of Immature Stages

The egg : The egg (Fig. 3) is translucent, creamy white with a perfectly smooth, shining, unsculptured surface. In shape it is elongate-ovate, slightly arched with a broad obtuse cephalic end and narrow caudal end. The eggs varied very widely in size from 1·9 mm. to 3·3 mm. in length, averaging 2·2 mm. for 10 eggs ; the width ranged from 0·5 mm. to 0·71 mm. averaging 0·54



TEXT-FIGS. 1–7.—Fig. 1. *Xoridescopus* (new species)—Adult female. Fig. 2. *Xoridescopus sp.*—abdominal tip and ovipositor (ventral view). Fig. 3. *Xoridescopus*—egg. Fig. 4. Primary larva (ventral view). Fig. 5. Primary larva (cephalic skeleton). Fig. 6. Second stage larva (dorsal view). Fig. 7. Second stage larva (cephalic skeleton).

mm. The egg period also varied appreciably during the period November to March when the species was under rearing in the laboratory. It ranged from

24 to 40 hours, averaging 30 hours for a dozen cases. In the process of hatching, the fully formed young larva emerges by breaking through the elastic chorion from the anterior ventral region leaving behind the irregularly split and collapsed empty egg shell.

First stage larva: The primary larva (Fig. 4) is of the usual ichneumoniform type. It is nearly pure white with a distinct broad head and cylindrical body of 13 segments tapering towards the caudal end. The head is comparatively well chitinised with a dorso-ventrally flattened capsule bulging laterally and is generally broader than the body. It is slightly brownish in colour with a pair of small papillæ like antennæ placed antero-dorsally. The body is apparently smooth and appears devoid of tubercles or spines or hairs. The digestive canal with its fore, mid and hind parts is visible through translucent cuticle. The pulsations of the heart are discernible. The fat body is not distinguishable at this stage but the tracheal system may be traced to some extent. The suctorial mouth is prominent and protruding on the ventral aspect of head. The cephalic skeleton and mouth parts may be visible under a binocular. The most prominent parts are the strong curved mandibles. The cephalic skeleton at this stage (Fig. 5) consists of the supporting mandibular struts (superior and inferior connected together by the arched pleurostoma. These latter are continued anteriorly to form the semicircular epistoma. The clypeal arch is not quite distinct. The pleurostomal rami are drawn backwards to form the hypostoma. The tentorium which connects these latter is not distinct at this stage. The transparent fleshy lobes of maxillæ below the mandibles are not very clear and the beginnings of the bilobed labium may be indistinctly traced. The salivary duct is present but not pronounced. A few setæ on the cuticle around the mouth region may be visible. These parts of the head skeleton attain their full development and complexity in the course of the succeeding three instars. The larva is active and effects quick movements. Often more eggs than one are laid and therefore two or more larvæ are hatched on same host but never more than one larva survived till the next instar. Usually the older or the earliest hatched or the strongest larva survives, the rest being destroyed by competition and actual fight. Several trials with two or more larvæ have been made in cages and watched under a binocular. The larvæ fight with each other and either or both are dead. In two cases under observation the fight was so severe that both succumbed due to injuries caused by mouth parts. In no case was found more than one larva surviving beyond the first stage on the same host. The larva measures from 1·95 mm. to 3·4 mm. averaging 2·5 mm. in length ; and 0·45 to 0·54 mm. averaging 0·5 mm. in width ; the head capsule varies from 0·55 to 0·62 mm. averaging 0·57 mm. The larva undergoes the first moult within about 12-16 hours of hatching.

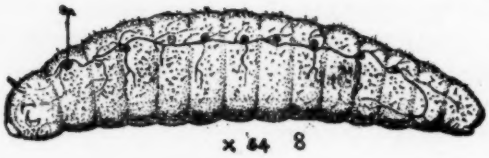
Second stage larva : The larva at this stage (Fig. 6) differs from the previous stage not only in size, shape, appearance and colour but also in head and cephalic skeleton. The larva is more elongate and cylindrical with the head slightly smaller and narrower than body. The general colour is yellowish white with the coloured gut and creamy granular fat bodies visible through the cuticle. The cuticular surface appears to be rough being covered with minute setæ. The head and mouth parts (Fig. 7) are weaker and less sclerotised at this stage. The epistoma is thinner and less conspicuous. The larva measures from 2·7 mm. to 4·7 mm. averaging 3·5 mm. in length and 0·62 mm. and 0·85 mm. averaging 0·70 mm. in width ; the head varies from 0·56 mm. to 0·61 mm. averaging 0·58 mm. This stage occupies one to two days.

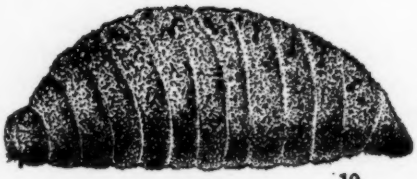
Third stage larva : This stage (Fig. 8) differs little from the second one except in size. The mandibles and other cephalic structures (Fig. 9) have increased in size. The colour is more dull and the fat bodies are larger and more conspicuous. Length varies from 4·3 mm. to 6·2 mm. averaging 5·1 mm.; width from 0·75 mm. to 1·4 mm. averaging 1·0 mm. ; head 0·65 mm. to 0·8 mm. averaging 0·7 mm.

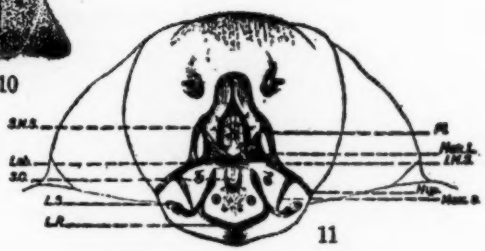
Final stage or mature larva : The mature larva (Fig. 10) is much larger in size and has assumed a typical ichneumonid form. It has an arched dorsal surface and somewhat flattened ventral surface. It is of a dull cream or yellowish colour with the dark gut and large elongate fat bodies prominent. The cuticle is very rough and prickly with setæ and spines of varying sizes (Fig. 12). The head is much smaller in comparison with the body. The spiracles (Fig. 13) in meso and meta thorax and the seven abdominal pairs with the longitudinal trunks are well developed and conspicuous. The head is slightly convex dorsally with the strongly chitinised and pigmented mouth parts and skeleton conspicuous ventrally.

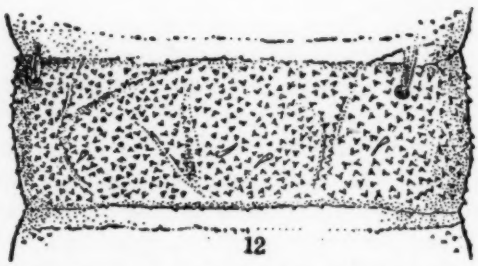
Mouth parts : (Fig. 11) The cephalic skeleton at this stage is very characteristic in being heavily chitinised and pigmented. Though the general arrangement is somewhat similar to that of first stage larva, the parts as a whole are well developed with the addition of certain new structures followed by the disappearance of a few others. The mandibles are strong, sharp and pointed and are supported by the superior and inferior mandibular struts. The epistomal arch connecting the two superior struts has disappeared. The inferior strut is only a projection of the curved hypostoma. The pleurostomal rami connect the struts, superior with the inferior. The maxillary lobes are supported by maxillary struts which are mere curved prolongations of the hypostoma. On the lower border of the mouth is found the labial ring which is somewhat horse-shoe-shaped. The labial ring is supported on

either side by the labial struts. The labium connects the open ends of the the labial ring wherein the salivary duct opens. The lateral and the anterior borders of the mouth are bounded by the maxillary lobes and the labrum.









TEXT-FIGS. 8–13.—Fig. 8. Third stage larva (side view showing spiracles and trachea system). Fig. 9. Third stage larva (cephalic skeleton). Fig. 10. Mature larva (side view). Fig. 11. Mature larva (cephalic skeleton). *Ep.*, Epistoma ; *Hyp.*, Hypostoma ; *I.M.S.*, Inferior mandibular strut ; *L.M.*, Labrum ; *Lbr.*, Labial ring ; *L.S.*, Labial strut ; *MXL.*, Maxillary lobes ; *MXS.*, Maxillary struts ; *P.S.*, Pleurostoma ; *S.M.S.*, Superior mandibular strut ; *S.O.*, Salivary opening. Fig. 12. Thoracic segment (dorsal view). Fig. 13. Thoracic spiracle (enlarged).

The edges of the labrum bear pairs of setæ and sensory pits. Setæ are also borne by the maxillary lobes. Besides these setæ, the maxillæ as well as the labium bear traces of a pair of maxillary palps and labial palps which are represented by sensory pits surrounded by chitinous rings shaped like Fig. 8. The size of the mouth parts, the disposition of setæ and sensillæ are distinguishing characters of the species. Among these structures the labial ring

and struts, the maxillary struts, the labial and maxillary sensory papillæ form new structures developed in the mature larva.

The duration of this stage may extend upto a period of seven days but averaged about two days before starting cocooning. By this time the host larva is reduced to an empty cuticle and head capsule. The larva ranged from 7·5 mm. to 8·5 mm. in length averaging 8·0 mm. ; from 1·9 mm. to 2·1 mm. averaging 1·95 mm. in width. The head measurements varied from 0·85 mm. to 0·9 mm. averaging 0·87 mm.

The cocoon : The full grown larva normally within two days sometimes extending upto eight days begins to spin a cocoon. The cocoon is thin, papery, cylindrical and is almost semi-transparent. The cocoon is formed within the tunnel made by the host in the stem. With this, the mature larva has passed on to the prepupal stage.

Prepupa : This stage in this species is remarkable. It passes through two distinct phases or types of form before it actually turns to a pupa, as in *Exenterus abruptorius* (Morris, 1937). The first of these prepupal stages corresponds to the *eonymphal* stage. The shape is similar in general appearance to that of mature larva but is to some extent contracted in length and averages about 7·5 mm. in length. It is only capable of slight side to side movement. The large mouth parts are still clear but not useful for feeding. The colour becomes dull and dirty white. The segmentation of the body is not so marked as in the mature larva. It shows no activity of any kind. This condition lasts for about two days when it passes on to the next phase—the *pronymphal* stage. The beginning of this stage is marked by the appreciable swelling of the abdomen and the separation of the body into thorax and abdominal regions by a constriction. The head and thorax are not well separated. The body has become somewhat lengthened and much curved on the ventral aspect. The imaginal eyes have begun to appear. It passes one or two days in this stage and voids the larval meconium. At the same time it casts away the last larval skin and turns to a white Ichneumoniform pupa.

Pupa : It is pure white when freshly formed with pinkish eyes. It soon attains a yellowish tint followed by light brown. The mandibles also turn brown. Two days prior to emergence the pupa becomes dark and assumes the general markings and form of the adult. On exposure of the cocoon by opening the stem the pupa becomes extremely active and revolves rapidly on its axis for several minutes. When fully formed the adult breaks open the pupal skin, bites a hole at the cephalic ventral aspect of the cocoon first and then through the stem so as to emerge out. The prepupal and pupal periods occupy from 14 to 21 days averaging 18·1 days for 12 individuals.

Development and Life-Cycle

There is considerable lack of uniformity in the development and many instances were observed when the development was retarded mainly in the larval or pupal periods. The egg period was fairly uniform within the range of one day to a little less than two days, averaging about 30 hours. The larval period varied from 5 to 13 days extending even upto 18 days but averaging 8·4 days. The prepupal stage including its two phases ranged from 3 to 5 days, averaging 4 days made up of 3 days for eonymphal and one day for pronymphal stages. The pupal period proper ranged from 10 to 16 days averaging 13·7 days. The total life-cycle ranged from a minimum of 23 to 30 days averaging 27 days. The life-cycle period of the male was always two to three days shorter than that of the female.

Parthenogenesis

Experimental trials have shown that the species can reproduce parthenogenetically. In a set of three trials virgin unfertilised females were isolated on emergence from cocoons in cages with a supply of amaranthus stalks loaded with unparasitised host grubs. Oviposition resulted in both the cases and the progeny developed into males.

Sex Ratio

Out of 15 adults whose sexes were recorded, six happened to be females. The number is too few to arrive at a correct appreciation of the proportion of sexes in nature. But yet an indication may be traced from this that the ratio may be somewhere near 40% females and 60% males.

Longevity of Adults

The life of the adult female was tested in a series of cases with a supply of food in the shape of sugar solution. It varied from 10 to a maximum of 67 days, averaging 29·3 days for 12 individuals. The longevity of males was seen generally to be much reduced, varying from 7 to 39 days, averaging 22·3 days.

Seasonal Occurrence

The studies so far made have shown that the parasite does not occur throughout the year. The species appears to occur during the season—November to March. Even during this period it is not of great abundance. The peak of its comparative abundance is during the month of December. The percentage of parasitism from rough computations may not be appreciable but it may be safe to conclude that the species is an important ecolgical factor in the balance which is maintained in the complex of host-parasite association.

Acknowledgments

The writer is indebted to the Government Entomologist, Coimbatore, for the facilities afforded for these studies.

Summary

In exploring the possibilities of biological control of the cotton stem weevil of South India, some attention was directed towards the study of the biology and natural ememies of allied curculionids of similar habits. Among such forms, the common Amaranthus weevil of South India, *Hypolixus truncatulus* B. proved to be the most useful laboratory host for many species of parasites. An account of this weevil and its parasites was presented before the Science Congress session (Calcutta, 1938).

Since then, the studies have been continued, though intermittently, and a few new and interesting species of parasites have been encountered. One such species forms the subject of this short paper.

The parasite in question is a new species of Ichneumonid belonging to the genus *Xoridescopus*. An account of this parasite together with its life-history and habits is furnished.

It is a primary ectophagous larval parasite of *Hypolixus truncatulus* B. preferring the late third and fourth instars of the host grubs for parasitisation. It has a few other hosts which are all stem-boring weevils. The parasite stings and completely paralyses the host before oviposition with a maximum capacity of 34 eggs per fertilised female in captivity. On account of intense larval fight, never more than one larva was seen to survive beyond the first stage on a single host. The total life-cycle covered an average of 27 days made up of an egg period of about 30 hours, larval period of 8·4 days, a prepupal period of 4 days and a pupal period of 13·7 days. The length of life of adults never exceeded 67 days. Detailed descriptions of the immature stages, the nature and development of cephalic skeleton and mouth parts and the prepupal phases have been presented since these form the most characteristic and distinguishing features of the species.

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INHERITANCE OF FLOWER COLOUR IN *SALVIA COCCINEA* JUSS EX MURR.

By L. S. S. Kumar

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The genus *Salvia* comprises a number of species which are grown for their ornamental flowers since they make ecxellent and showy borders in gardens. One of the species most commonly grown is *Salvia splendens*, which bears racemes of bright scarlet flowers of large size. *Salvia coccinea* Juss ex Murr., which is less commonly grown, has much smaller flowers of the same colour and brilliance as that of *S. splendens*.

From reference to literature, it is observed that the genus *Salvia* has not been utilized to much extent in genetic investigations although the genus has been used in studies on taxonomy, pollination and other allied botanical aspects. References to work bearing on genetics of *Salvia* include only that of Blaringhem's (1935) observetion on the occurrence of unilateral or maternal inheritance in a cross between *S. memorosa* and *S. sclarea*, and Schnack's (1941) success in producing a tetraploid *S. splendens* by colchicine treatment.

The material used for this study included two varieties of *S. coccinea*, namely the scarlet, and the light pink-flowered types. The scarlet-flowered type, which had been grown for some years, suddenly mutated and produced a light pink-flowered type. The mutant and its parent differed in respect of flower colour only and for no other plant character (Kumar, 1942). To determine, therefore, the type of mutation for flower colour and the manner of inheritance of this character, a cross was made between the scarlet-flowered parental type and the light pink-flowered mutant type in 1940. The progenies up to F_3 and from back-cross together with the parents were grown during 1942 in two lots. The first lot, comprising the F_1, F_2 and back-cross, was grown during the hot months of March to May, and the second lot, which included all the generations of the first lot, plus the F_3 was grown during the rainy months from June to September 1942. The earlier trial had a smaller proportion of the progenies due to prevalence of adverse weather conditions. Some difficulty was encountered, however, during both the trials to obtain satisfactory germination of the hybrid seeds. When the seeds were sown directly into the soil either in the pots or in plots, they either did not germinate at all, or if they did, germination was very poor. Therefore, the seeds were germinated with care in enamel dishes lined with moist blotting papers, which were kept in glass-walled cabinet inside the laboratory. After a majority of the seeds had germinated and produced the first pair of true leaves, they were transferred to earthen pots by removing them entirely with the

blotting paper which was then placed on the flattened soil surface. Later, by means of a stout iron needle, holes were punctured in the blotting paper in between the seedlings to enable easy penetration of their roots. Next, the roots were covered by a thin layer of earth. By this method a high percentage of germination and survival of the seedlings was ensured. After another six weeks, when the seedlings had produced several pairs of leaves and had grown to 2" height they were transferred to prepared beds in the garden.

There was no difference in flower colour of F_1's from reciprocal crosses and their flower colour resembled that of the scarlet-flowered parent. The scarlet flower colour was thus observed to be dominant, and further the cross revealed that the pink-flowered type arose due to the gene responsible for scarlet flower colour mutating in a recessive manner to produce the pink-flowered type.

Since the data of the small-scale summer trial perfectly agreed with the data of the large-scale trial during the rains, the latter alone is given in the following tables :—

TABLE I

Segregation for flower colour in F_2 progenies

Cross		Scarlet	Pink	X^2	P	Remarks
Pink × Scarlet ..	Observed	129	44	0·0174	0·9–0·8	Very good fit
	Expected on 3 : 1	129·75	43·25			
Scarlet × Pink ..	Observed	123	33	1·23	0·3–0·2	Fair fit
	Expected on 3 : 1	117	39			
Total ..	Observed	252	77	0·447	0·7–0·5	Good fit
	Expected	246·75	82·25			

TABLE II

Segregation for flower colour in progenies of the back-cross

Cross		Scarlet	Pink	X^2	P	Remarks
Pink × F_1 (P × S) ..	Observed	81	80	0·006	0·95–0·9	Very good fit
	Expected on 1 : 1	80·5	80·5			
Pink × F_1 (S × P) ..	Observed	61	80	2·56	0·22–0·1	Fair fit
	Expected on 1 : 1	70·5	70·5			
Total ..	Observed	142	160	1·072	0·3	Fair fit
	Expected	151	151			

From Tables I and II, it will be seen that the observed F_2 and back-cross ratios show a good to fair fit of the 3 : 1 and 1 : 1 ratio respectively expected on a single gene difference.

TABLE III

Segregation for flower colour in F_2 progenies

F_2		F_3					
Plant No.	Flower colour	Scarlet		Pink	X^2	P	Remarks
12	Scarlet ..	Observed	32	9	0·203	0·7–0·5	Good fit
		Expected on 3 : 1	30·75	10·25			
43	„ ..	Observed	27	8	0·085	0·8–0·7	Good fit
		Expected	26·25	8·75			
47	„ ..	Observed	22	8	0·044	0·9–0·8	Very good fit
		Expected	22·5	7·5			
48	„ ..	Observed	19	5	0·22	0·7–0·5	Good fit
		Expected	18	6			
49	„ ..	Observed	22	10	0·666	0·5–0·3	Fair fit
		Expected	24	8			
92	„ ..	Observed	21	11	1·5	0·3–0·2	Fair fit
		Expected	24·75	8·25			
96	„ ..	Observed	32	10	0·32	0·9–0·8	Very good fit
		Expected	31·5	10·5			
152	„ ..	Observed	30	10	..	..	Perfect fit
		Expected	30	10			

TABLE IV

Segregation for flower colour in F_2 progenies

F_2		F_3		
Plant No.	Flower colour	Scarlet	Pink	Total
5	Scarlet	32	..	32
13	„	26	..	26
88	„	13	..	13
89	„	36	..	36
45	Pink	..	35	35
67	„	..	39	39
155	„	..	33	33
165	„	..	35	35

By considering Tables III and IV together, it will be observed that out of a total of sixteen selfed F_2 individuals comprising twelve scarlet and four pink types, selected at random and tested for their breeding behaviour in respect of flower colour in the F_3, one quarter or four have bred true for scarlet colour; another one quarter or four have bred true for light-pink flower colour ; and the remaining half or eight have segregated into scarlet and pink-flowered individuals. This agrees with the expected behaviour in F_3 of monogenic inheritance. The Chi-square and P values of F_3 segregating families show a better goodness of fit than even the F_2 and back-cross segregates. The observed F_2, back-cross and F_3 ratios clearly show that the flower colour in *S. coccinea* is inherited on a monogenic basis. The scarlet flower colour is a complete dominant to pink flower colour, and the pink has arisen from a recessive mutation of the gene for scarlet flower colour.

S. coccinea has been found to be an extremely suitable material for demonstrating to students simple mendelian inheritance. The cross between the two varieties is very easily made, and a single F_1 individual produces many hundred seeds. The plants come into flower six weeks after transplanting. Further, because of the small size of the plant several hundred plants could be accommodated in a small space. Even a small F_2 population gives a clear-cut 3 : 1 ratio. All these advantages recommend it as a most suitable and convenient material for demonstrating mendelian inheritance.

Summary

It is shown that the pink-flowered type has arisen by a recessive mutation of the scarlet type. The inheritance of scarlet and pink flower colours in *S. coccinea* Juss ex Murr. follows a monogenic inheritance.

The suitability of this species for demonstrating simple mendelian inheritance is explained.

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AN ECOLOGICAL STUDY OF A GARDEN POND CONTAINING ABUNDANT ZOO-PLANKTON*

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(With one graph and two tabular statements)

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1. Introduction

The ponds in the city of Madras which do not dry up completely during the south-west monsoon season may be roughly divided into three groups : (i) those containing abundant macrophytic vegetation without any phyto- and zoo-plankton, (ii) those containing abundant phyto-plankton and/or zoo-plankton, and (iii) those containing both macrophytic vegetation and phyto- and zoo-plankton. Three ponds, each representing typically one of these groups were studied simultaneously for a year during 1934–35. The studies of the pond representing the first group[11] and of the pond representing the second group—containing abundant phyto-plankton without any macrophytic vegetation[10] have already been published.

In this paper is given an account of the changes in the physical and chemical variables of a garden pond containing abundant zoo-plankton. This pond, according to the above classification, will also come under the second group of ponds found in the city. It was studied simultaneously with the other two ponds. Data relating to habitats of the above types of ponds in the tropics are lacking (Bharadwaja[5]) and hence these studies will be of scientific interest apart from their importance to tropical pisciculture.

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2. *The Environment*

(*a*) *The location, shape and size*

This pond is situated in the south-west corner of a bungalow called " Allatur Villa " in Poonamalee High Road. It is 44 feet long and 40 feet broad, so that it looks like a circular pond. It has a maximum depth of about 15 feet at the centre at its full pond level during the north-east monsoon season. It is connected to a well on the eastern side, from which water is baled out daily from 7 to 11 A.M. by means of a pikotah, for gardening and watering the cocoanut trees inside the compound. On the eastern side, the tops of about a score of cocoanut trees prevent the sun's rays from falling upon the surface of the water in the pond till about mid-day. It is provided with two flights of steps, one on the northern side and the other on the southern side for the servants to get down safely into the pond for bathing, washing clothes and cleaning kitchen vessels, as it has precipitous sides, which are covered with grass, when the level of water goes down gradually in the summer and the south-west monsoon season.

(*b*) *Collection of samples*

Samples of water were collected just below the surface of water from one and the same place between 9–30 and 11–30 A.M., at intervals of a fortnight or once a month between February 1934 and January 1935. Bottles and reagents required for the determination of the dissolved gases and pH were taken in a carriage and examined on the spot. A Winchester-quart full of water was taken to the laboratory for other chemical tests which were immediately carried out.

(*c*) *The meteorological data*

They were obtained from the Madras Observatory and have been described already (Ganapati, 1941, pp. 56–57).

(*d*) *Physical variables*

(i) *Colour.*—The colour of water as it appeared to the naked eye at the time of sample collection was recorded. The water was dirty yellowish green in February, dark green on 8th March, greyish on 22nd March, July, August and September, brownish on 11th April, dark brown in the latter half of April, May and June, and greenish in November, December and January 1935.

(ii) *Temperature.*—The temperature of the surface water was measured by means of a surface thermometer graduated from 0–50° C., each degree being subdivided to a fifth of a degree. The temperature was found to vary

TABLE I A

" Allatur Villa " Garden Pond, Madras

TABLE I A

"Allatur Villa" Garden Pond, Madras

Date	Time of collection	Temp. °C.	D.O. in c.c./l	% Sat.	Mg. per 100 c.c.			pH	Trans-parency in cms.	Colour of water	*Meteorological Conditions
					Free CO_2	CO_3	HCO_3				
22—2—34	10–15 A.M.	29·6	2·77	49·4	0·33	Nil	16·78	7·7	69·0	Dirty yellowish green	B.S.S.–C.B.S.–N:W.
8—3—34	10-00 A.M.	29·8	4·32	77·3	0·44	,,	16·93	7·8	36·0	Dark green	do.
22—3—34	10–15 A.M.	31·5	1·89	..	0·66	,,	18·76	7·8	53·5	Greyish	do.
11—4—34	10-00 A.M.	30·4	0·34	6·1	0·88	,,	22·58	7·8	..	Brownish	do.
27—4—34	10-00 A.M.	32·0	0·52	..	0·66	,,	26·38	7·7	..	Dark brown	do.
26—5—34	9–30 A.M.	31·8	0·81	..	0·88	,,	24·10	7·7	..	do.	do.
21—6—34	10-00 A.M.	29·4	1·03	18·3	1·32	,,	25·01	7·6	..	do.	do.
14—7—34	10-00 A.M.	30·5	0·61	11·0	1·32	,,	28·67	7·8	..	Greyish	do.
8—8—34	11–15 A.M.	30·8	1·04	23·8	0·67	,,	22·27	7·7	..	do.	C.S.–N.B.S.S.–N.W.–Good rainfall two dyas previously
22—8—34	10–45 A.M.	29·0	0·73	12·9	0·66	,,	21·35	7·7	..	do.	C.S.–N.B.S.S.–N.W.
6—9—34	10–30 A.M.	29·8	1·78	33·9	0·44	,,	21·35	7·7	..	do.	do.
19—9—34	10-00 A.M.	31·1	1·38	..	0·44	,,	17·99	7·7	..	do.	B.S.S.–C.B.S.–N.W.
25–10–34	10-00 A.M.	28·9	1·65	29·1	0·55	,,	21·65	7·7	..	do.	C.S.–N.B.S.S.–N.W.
23–11–34	10-00 A.M.	26·6	4·77	81·1	0·55	,,	24·55	7·7	..	Greenish	do.
13–12–34	10–15 A.M.	24·8	2·15	35·5	0·22	,,	21·04	7·7	..	do.	do.
30—1–35	10·20 A.M.	27·4	1·76	37·0	0·66	,,	21·04	7·6	..	do.	do.

* B.S.S.—Bright Sunshine ; C.B.S.—Clear Blue Sky ; C.S.—Cloudy Sky ; N.B.S.S.—Not bright Sunshine ; N.W.—No wind ; S.W.—Slight wind.

TABLE I B

" Allatur Villa " Garden Pond, Madras

Date	Parts per 100,000														
	Hardness			Chlorides	Am. N	Alb. N	Nitrous N	Nitric N	Oxygen absorbed	Total solids	Fixed solids	Ignitible matter	Phosphates	Silicates	Iron
	Total	Perm.	Temp.												
22—2—34	28·0	17·0	11·0	27·5	0·028	0·038	Nil	Nil	0·174	78·6	63·4	15·2	Nil	1·00	0·05
8—3—34	30·0	16·0	14·0	30·5	0·018	0·056	,,	,,	0·229	81·8	64·8	17·0	,,	1·00	0·05
22—3—34	32·0	17·0	15·0	31·5	0·090	0·084	,,	,,	0·257	85·2	66·4	18·8	0·001	1·00	0·05
11—4—34	36·0	20·0	16·0	35·0	0·100	0·084	,,	,,	0·290	109·2	76·4	32·8	Nil	1·50	0·08
27—4—34	40·0	21·0	19·0	39·5	0·224	0·095	,,	,,	0·257	119·8	97·2	26·6	0·001	1·60	0·08
26—5—34	44·0	28·0	16·0	54·5	0·146	0·095	,,	,,	0·301	135·4	113·2	22·0	0·001	2·50	0·08
21—6—34	46·0	33·0	13·0	78·5	0·224	0·120	,,	,,	0·316	156·4	128·8	27·6	0·001	2·70	0·08
14—7—34	50·0	34·0	16·0	71·5	0·012	0·080	,,	,,	0·576	177·2	141·6	35·6	0·009	3·50	0·07
8—8—34	46·0	30·0	16·0	43·3	0·064	0·072	,,	,,	0·297	144·2	110·2	34·0	0·003	3·00	0·08
22—8—34	44·0	32·0	12·0	45·44	0·288	0·080	,,	,,	0·327	171·0	115·8	55·2	0·001	2·80	0·10
6—9—34	44·0	26·0	18·0	40·8	0·180	0·096	,,	,,	0·286	154·0	102·8	51·2	0·003	2·26	0·02
19—9—34	42·0	26·0	16·0	38·60	0·224	0·096	,,	,,	0·295	142·4	111·6	30·8	0·002	2·00	0·02
25-10-34	40·0	25·0	15·0	38·62	0·240	0·160	,,	,,	0·318	133·2	105·6	27·6	0·003	2·80	0·015
23-11-34	40·0	23·0	17·0	38·77	0·080	0·080	trace	,,	0·200	126·4	108·0	18·4	0·005	2·75	0·01
13-12-34	38·0	25·0	13·0	40·23	0·088	0·096	Nil	,,	0·193	122·4	106·8	15·6	0·002	2·40	0·01
30—1—35	38·0	22·0	16·0	43·31	0·080	0·080	,,	,,	0·250	137·2	110·8	26·4	0·001	2·80	0·09

from 24°·8 to 32° C. Very probably this does not represent the maximum range, since the observations were made between 9-30 and 11-30 A.M., *i.e.*, in the forenoon.

The temperature of the surface water was highest (32° C. on 27th April) in the hot weather and least (24·8° C. on 13-12-1934) in the north-east monsoon season. It was found to increase gradually from February to April, when the maximum was reached, and later decreased till June, and increased again till September and thereafter it fell till December when the minimum was reached. Finally it began to increase again from December to January 1935.

These results with the mean daily temperature for each month are shown graphically in Fig. 1 from which it will be evident that the temperature changes in water follow closely those of the atmosphere.

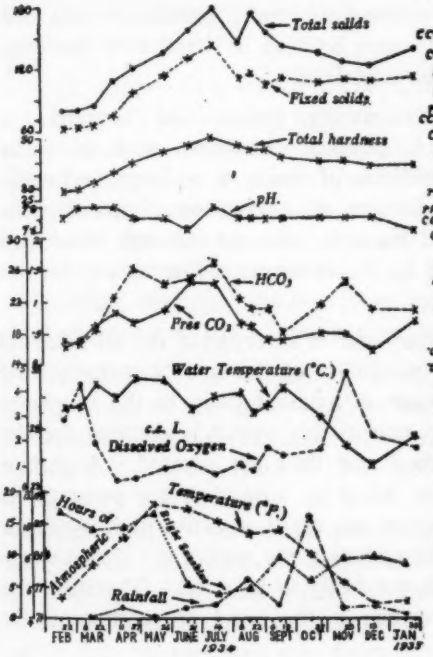

FIG. 1

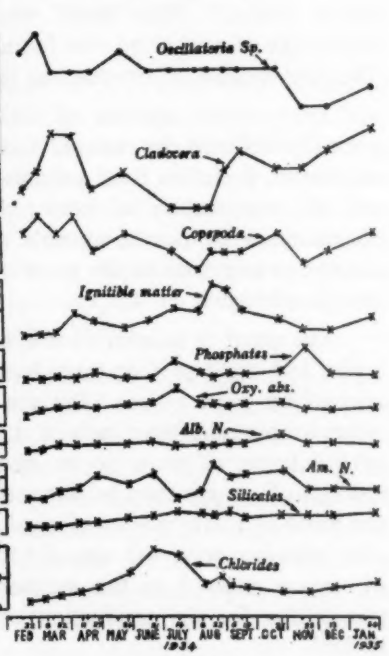

FIG. 2

Graph showing the physico-chemical variables of a garden pond containing abundant zoo-plankton

(iii) *Water level.*—As there was no facility for measuring accurately the depth of the pond, it was not measured. The level of water was,

however, at its maximum in February and minimum in September; it was found to decrease gradually from February to September and to increase again till the second maximum was again reached in January 1935.

(*e*) *Chemical variables*

(i) *Dissolved oxygen.*—This was estimated according to Rideal and Stewart's modification[14] of the Winkler's method. The oxygen content was found to vary between a minimum of 0·34 c.c./l. on 11th April and a maximum of 4·77 c.c./l. on 23rd November. It was found to be greatest during the north-east monsoon and least during the south-west monsoon season; and to decrease generally from February till 22nd August and thereafter to increase till 23rd November and to decrease again till 30th January 1935.

The values for percentage oxygen saturation were calculated from Fox's[9] tables. The water was throughout under-saturated and the percentage of saturation was found to vary between 6·1 and 81·1 per cent. The low content of oxygen has to be explained.

The oxygen content of lakes, reservoirs, ponds and streams are normally affected by several factors; physical conditions such as water movement, pollution from animals, addition of spring or underground water and the temperature of water; production of oxygen by plants, and its consumption by plants, animals and bacteria. So the amount of oxygen present at any time in the pond will be the resultant of the several factors mentioned above.

The pond is located in one corner and is surrounded on all sides by walls and trees so that there is no possibility of the surface water getting aerated by wind action. But the water is agitated daily in the mornings when people take their bath in it, so that in this way it is possible for the several layers of water to be disturbed and thus get aerated. A certain amount of oxygen may be obtained in this way. Besides, the presence in the pond of a few species of algæ, which can carry on active photosynthesis after mid-day only, will also aid in oxygenating the water; but the quantity of oxygen received in this manner is not likely to be great. Therefore the possibilities for the production of oxygen in the pond are comparatively limited.

On the other hand, the possibilities for consumption appear to be greater. The pond receives daily fresh underground water from the well near by, after the well water has been baled out and does not usually contain any oxygen, so that the final mixture of waters in the pond will naturally contain less of oxygen than what it possessed before the addition of the spring water.

Again, the pond supports an abundant growth of zoo-plankton which must consume a good lot of the oxygen dissolved in the pond water, while alive and after death. Thirdly, the pond is also polluted very badly by kitchen wastes and by the washing of dirty clothes. Thus, the organic content and the bacterial pollution of the water increase daily. Therefore the processes of absorption of oxygen predominate over those that produce it, with the result that the pond remains under-saturated at all times.

Comparing the oxygen values for the hot weather and south-west monsoon season with those for the north-east monsoon season and cold weather period, it is found that the oxygen content in the case of the former is lower than in the case of the latter. This may be due chiefly to the metabolic demands of the aquatic animals for oxygen increasing with the increase of temperature, and resulting in the low oxygen content in the first period. This inference is supported by the increased free CO_2 content in the same period.

(ii) *Free CO_2.*—Free CO_2, CO_3 and HCO_3 ions were estimated according to A.O.A.C.[1] method. Free CO_2 was found to vary from a minimum of 0·22 to a maximum of 1·32 parts per 100,000. It was found to increase gradually from February to June, when the maximum was recorded, remained at the same level in July, and decreased till December when the minimum was reached. Its presence in comparatively smaller amounts during the hot weather may be due to its partial utilisation by the chlorophyll-bearing organisms; and this is borne out by the comparatively high oxygen and pH values during the same period.

Free CO_2 was present in fairly large amounts throughout the year. Its presence in this pond may be explained as follows: Plant life is poor while animal life is abundant. The pond is shaded for about six hours daily so that the photosynthetic activity in the pond is very low while the respiratory activity must be great. It is also highly contaminated with organic matter. Therefore, under these circumstances, the factors responsible for the absorption of oxygen must be greater than those that discharge it, with the result that organic matter is decomposed by bacteria and free CO_2 is liberated in large amounts at all seasons of the year. A portion of it may be obtained also from spring water, which is usually saturated with it.

(iii) *CO_3 ions.*—They were absent, as free CO_2 was always present in large amounts. Their absence, therefore, indicates again that photosynthesis was feeble and that animal life was considerably greater than plant life in the pond.

(iv) *Bicarbonate* (*HCO_3*) *ions*.—The curve for HCO_3 ions runs almost parallel to that for "free CO_2". Bicarbonates varied from a minimum of 16·78 parts in February to a maximum of 28·67 parts in July. They were found to increase gradually from February to July and to decrease later from July to 19th September and to increase thereafter till 23rd November and to decrease again till 30th January 1935.

A study of the curves and the data for free CO_2, bicarbonates and dissolved oxygen shows that the year can be roughly divided into two periods: the first period from February to July, when free CO_2 and bicarbonates were generally increasing while the oxygen content was decreasing (exceptions being 8th March and 21st June); and the second period from August to December 1934, when free CO_2 and bicarbonates were decreasing generally while dissolved oxygen was increasing. The first period may be considered as one of greater reduction of organic matter than the second.

(v) *pH*.—The pH of the pond water was determined colorimetrically by means of a Hellige comparator using phenol red as indicator. This was found to fluctuate within very narrow limits: 7·6 to 7·8 units. It was found to increase slightly from February to 11th April and to decrease later till 21st June and subsequently to increase slightly till 14th July and to decrease again and thereafter to remain constant till 12th December. The slight increase in pH during February to April when the temperature is high and the hours of bright sunshine are longer would seem to show the feeble photosynthetic activities of the chlorophyll-bearing organisms in the water. This inference is also supported by the comparatively higher figures for dissolved oxygen and lower figures for free CO_2 during the same period.

Atkins and Harris[4] state that pH values below 8·1 indicate an excess of carbon dioxide above the amount in equilibrium with that of the air, so that a value such as pH 7·6 denotes a considerable excess, probably accompanied by a reduced percentage of oxygen. This observation is too true in this pond. The low pH values throughout also explain the low oxygen content of the water. In other words, the fact that the pH values never reached 8·1 indicates that the respiratory processes were greater than the photosynthetic process.

The curves and the records for free CO_2, bicarbonates (HCO_3), dissolved oxygen and pH show intimate relationship. With the increase of free CO_2, bicarbonates and pH, there is a general decrease of dissolved oxygen, from February to July; and again with the general decrease of free CO_2, bicarbonates and pH there is an increase of dissolved oxygen, from August to

December. These observations are in consonance with the fact mentioned previously that the reduction of organic matter is probably greater during the first period than during the second period. Temperature in the first period and rainfall or level of water in the second period seem to play a great rôle.

(vi) *Total and fixed solids.*—These were estimated as per Thresh *et al.*[17] The figures for the total solids varied from a minimum of 78·6 parts per 100,000 in February to a maximum of 177·2 parts in July and the fixed solids from a minimum of 63·4 parts in February to a maximum of 141·6 parts in July.

The records and the curves show that the total solids were highest during the south-west monsoon season and least during the preceding hot weather, and that they increased gradually from February to July when the maximum was reached and decreased thereafter till the second minimum was reached in December.

The fixed solids also showed a similar rise but the second minimum was reached earlier in October and later increased again in January.

A definite relationship can be traced between the total and fixed solids on the one hand and the pH on the other, especially during February to April, in spite of the narrow pH range (0·2 unit). It is during this period that the pH values are comparatively high, while those for solids are low.

Also the figures for free CO_2, HCO_3 ions and total and fixed solids show intimate relationship. All these data increase from February to July, when the maximum for the year is recorded in each case. Later on, these figures show a general tendency to decrease from August 1934 to January 1935. The increasing figures during the first period are most probably due to decreasing level of water and to increased biological activity, resulting in increased free CO_2, bicarbonates and total and fixed solids in the water. The decreasing figures during the other period have probably to be ascribed to increasing level of water and to decreased biological activity in the pond.

(vii) *Total hardness.*—This was estimated by Clark's soap test as described by Notter and Firth.[13] The figures varied from a minimum of 28·0 parts in February to a maximum of 50·0 parts in July. It was found to be highest in the south-west monsoon season and least during the hot weather; it was also found to increase thereafter till January 1935 when the second minimum was reached. The pond water was "very hard" throughout the period of investigation.

The curves and the figures for total solids and total hardness show a fair degree of close relationship. The values for total hardness and total

solids were lowest during the hot weather and highest during the south-west monsoon season and occupied intermediate values during the north-east monsoon and cold weather periods. The low values for total hardness during the hot weather may be due to precipitation of the less soluble carbonates of calcium and magnesium or to their utilisation by the shell-forming organisms; and the increase during the south-west monsoon season to the dissolution of the carbonates by the increased free CO_2 content.

(viii) *Phosphates* (P_2O_5).—Phosphates were determined by the Atkin's modified method[3] of the coerulemolybdic method of Deniges. They were found to vary from a minimum of nil in February, 8th March and 11th April to a maximum of 0·009 part in July. They were low during the hot weather and cold weather periods and fairly high during the south-west monsoon season.

The presence of phosphates almost on all occasions may be due to the constant animal contamination of the pond water and also to the death and decay of the abundant zoo-plankton and molluscan fauna in the pond. Their absence during February to 11th April might be due to their consumption by the few chlorophyll-bearing organisms in the pond water.

In spite of the presence of phosphates in the water, the development of phyto-plankton was very poor which was perhaps due to the rays of the sun not reaching the surface water for the major part of the day, throughout the year.

(ix) *Silicates* (SiO_2).—Silicates were estimated according to Robinson and Kemmerer's modification[15] of the method of Dienert and Wandenbulcke.[7] The quantity of silicates varied from a minimum of 1·0 part in February and March to a maximum of 3·5 parts in July. This was found to increase from February to July and thereafter to fluctuate between 3·0 and 2·0 parts per 100,000.

There is no apparent correlation between silicates and pH in this pond.

(x) *Chlorides* (*Cl*).—This was determined by Mohr's method.[18] They were found to vary from a minimum of 27·5 parts in February to a maximum of 78·5 parts in June. They increased gradually from February to June and decreased later to the second minimum in September, increasing again till January. They were very high during the south-west monsoon season and low during the hot weather period. The high content of chlorides indicated animal contamination.

(xi) *Iron* (*Fe*).—Total iron was estimated colorimetrically according to standard methods of water analysis.[2] Total iron was found to vary from

a minimum of 0·01 part in November and December to a maximum of 0·1 part on 22nd August. This was found to increase from February to August, and to decrease later till December, and to increase thereafter till January. It was highest during the south-west monsoon season and lowest during the north-east monsoon season.

(xii) *Organic matter* (*Tidy's* 4 *hours test*) *and its decomposition products*—(*a*) *Oxygen absorbed.*—This was estimated by Tidy's four hours test.[16] It was found to vary from a minimum of 0·174 part in February to a maximum of 0·576 part in July. The organic content was least during the cold weather period and highest during the south-west monsoon season and it was found to increase gradually from February to July, and to decrease thereafter (though not regularly) till the second minimum was reached in December and to increase again in January 1935.

(*b*) *Ignitible matter.*—This was obtained by difference of the values for total and fixed solids. It was found to vary from a minimum of 15·2 parts in February to a maximum of 55·2 parts on 22nd August ; it was lowest in the cold weather period and highest during the south-west monsoon season and was found to increase from February to 22nd August and to decrease thereafter till the minimum was reached in December.

The records and curves for " oxygen absorbed " and " ignitible matter " are almost similar barring minor differences due probably to methods of their estimation.

The curves for " total solids " and " oxygen absorbed " show striking resemblance. With the general increase of solids from February to July, the oxidisable organic matter also increases and later, with the decrease of solids from August to December the organic matter also decreases. The increasing figures from February to July may be due to the concentration of the pond water on account of decreasing water level and also to increased bacterial activity resulting in the increased degradation of the organic matter which is shown by the high figures for free CO_2, bicarbonates and low oxygen tension. The decrease of " solids " and " organic matter " during August to December might be due to dilution by rainfall.

(*c*) *Ammoniacal nitrogen.*—This was estimated by distillation and nesslerisation. It was found to vary from a minimum of 0·018 part on 8th March to a maximum of 0·288 part on 22nd August. The ammoniacal nitrogen content was lowest in the hot weather and highest during the south-west monsoon season, and it was found to increase from 8th March to 22nd August, and to decrease thereafter till the minimum was reached in January 1935.

(*d*) *Albuminoid nitrogen.*—This was estimated by distillation and nesslerisation of the remaining water (after distillation of ammoniacal nitrogen) and after adding alkaline permanganate, and nesslerisation according to the usual method. This was found to vary from a minimum of 0·038 part in February to a maximum of 0·16 part in October. It was lowest during the hot weather and highest in the north-east monsoon season ; and was found to increase gradually from February to June and to decrease till 8th August and to increase thereafter till October when the maximum was reached. Later it began to decrease till January.

(*e*) *Nitrous and nitric nitrogen.*—The former was estimated by the well-known Greiss-Ilosvay method and the latter by the phenol-disulphonic acid method. Except for one occasion in November when nitrous nitrogen was found in traces, both the substances were absent on all other occasions.

The increasing amounts of free and albuminoid ammonia from February to August or September may be due to concentration of water resulting from decreasing water level on account of evaporation and draw off for gardening purposes, and to the death and decay of zoo-plankton. In the end, organic matter in solution in the water is decomposed by bacteria resulting in high figures for free and albuminoid ammonia.

Although the pond is badly polluted and contains abundant zoo-plankton and molluscan fauna, nitrites and nitrates were conspicuous by their absence. It is quite likely that conditions unfavourable for nitrification were present in the pond. Their absence cannot be attributed to their utilisation by phyto-plankton or macrophytic vegetation both of which were insignificant.

3. *The Organisms*

Plankton collections were made with a view (1) to determine the periodicity of the population of the pond and (2) to trace the interrelationship between the variation in numbers of the flora and fauna on the one hand and the physical and chemical variables on the other. On each occasion a horizontal haul was made with a No. 25 fine net of silk bolting cloth (77 strands to a cm.) between the two opposite entrances to the pond. The net was towed carefully six times with the upper edge of the mouth just below the surface. Immediately after collection, the plankton in the net was emptied into a bottle, and the net was washed with the pond water and the washings also added to the bottle. The catch was then treated with enough neutralised formalin to make a concentration of 4 per cent.

A drop of the sediment from each tube was first examined qualitatively for phyto-plankton. The tube was then shaken and a drop of the turbid

liquid was examined microscopically under a one-inch square cover glass using a magnification of about 300. To maintain uniformity, the drop was taken each time from the same pipette. The frequencies of the phyto-plankton organisms present in each haul are expressed in symbols of Fritsch and Rich.[8] The numerical values to the various symbols are from counts of individuals found in 50 fields, so that *rrr* = 1; *rr* = 1–50; *r* = 50–100; *c* = 100–200; *cc* = 200–500; and *ccc* = over 500 organisms.

(*a*) *The Phyto-plankton*

Macrophytic vegetation was absent in the pond. Phyto-plankton was very poorly represented the catch consisting almost entirely of zoo-plankton. A carpet-like growth of blue-green algæ was seen covering the bottom on 14th July and algal patches which had probably peeled off from the bottom, were seen floating on the surface on 8th August when the level of water was very low. On other occasions no such floating matter was seen.

Three forms belonging to the Cyanophyceæ alone were noticed in the net plankton collection. They were *Microcystis flos-aquæ* (Wittr.) Kirchn., *Aphanocapsa sp.* and *Oscillatoria sp.* Of these three, the last was the most dominant organism, while the other two were found stray (*vide* Table II A).

Oscillatoria sp.—This was found to be abundant in 8th March, very common in February and May, common in 22nd March, April and June to October, very rare in November and December and rare in January 1935.

The abundance of *Oscillatoria sp.* especially during February to April may be correlated with the comparatively high oxygen content and pH value on the one hand and with the low figures for free CO_2, bicarbonates (HCO_3), phosphates, total and fixed solids and total hardness on the other, during the same period.

(*b*) *The Zoo-plankton*

The collections contained almost wholly of zoo-plankton. The bulk of the plankton consisted of Copepods and Cladocerans. The periodicities of the various groups are shown in Table II B.

Copepoda.—Six forms belonging to this group were found. The most dominant among them were *Neodiaptomus diaphorus* Kiefer and *Sinodiaptomus* (?) *indicus* Kiefer, while *Heliodiaptomus viduus* (Gurney) and *Neodiaptomus Schmackeri* (Poppe et Richard) were subdominant, and *Thermocyclops sp. nov.* and *Thermocyclops hyalinus* (Rehberg) were found stray.

Generally Copepods were abundant in 8th March and 11th April; very common in February, 22nd March, May, October and January 1935;

TABLE II A

Showing the Periodicity of the Phyto-Plankton in "Allatur Villa" Garden Pond, Madras

Serial No.	Name of the Organisms	22-2-34	8-3-34	22-3-34	11-4-34	27-4-34	26-5-34	21-6-34	14-7-34	8-8-34	22-8-34	6-9-34	19-9-34	26-10-34	23-11-34	13-12-34	30-1-35
A	**Cyanophyceæ—**																
1	*Microcystis flos-aquæ* (Wittr) *Kirchn*	*rrr*	..	..	..	..	..	..	..	..	..	..	..	..	..	*r*	*rr*
2	*Aphanocapsa sp.*	..	*rrr*	*rrr*	*rrr*	*rrr*	..	..	..	..	..	..	..	..	*rrr*	*rr*	*rr*
3	*Oscillatoria sp.*	*cc*	*ccc*	*c*	*c*	*c*	*cc*	*c*	*c*	*c*	*c*	*c*	*c*	*c*	*rr*	*rr*	*r*

TABLE II B

Showing the Periodicity of the Zoo-Plankton in "Allatur Villa" Garden Pond, Madras

Serial No.	Name of the Organisms	22-2-34	8-3-24	22-3-34	11-4-34	27-4-34	26-5-34	21-6-34	14-7-34	8-8-34	22-8-34	6-9-34	19-9-34	26-10-34	23-11-34	13-12-34	30-1-35
A	**Copepoda**	*cc*	*ccc*	*cc*	*ccc*	*c*	*cc*	Tube broken in transit to Europe	*c*	*r*	*c*	*c*	*c*	*cc*	*r*	*c*	*cc*
1	*Heliodiaptomus viduus* (Gurney)	*rr*	..	..	..	..	*c*		*c*	*c*	*c*	*c*	*c*	*cc*	..	*c*	..
2	*Neodiaptomus Schmackeri* (Poppe et Richard)	*rrr*	..	..	..	..	..		*c*	*c*	*c*	*c*	*c*	*cc*	..	..	*cc*
3	„ *diaphorus* Kiefer	*cc*	*ccc*	*cc*	*ccc*	*c*	*r*		*c*	*c*	*c*	*c*	*c*	*cc*	..	..	..
4	*Sinodiaptomus* (?) *indicus* Kiefer	*rrr*	*ccc*	*cc*	*ccc*	*c*	*c*		*c*	*c*	*c*	*c*	*c*	*cc*	..	..	*cc*
5	*Thermocyclops sp. nov.*	..	*rrr*	..	*rrr*	..	..		..	..	..	..	..	..	..	..	..
6	„ *hyalinus* (Rehberg)	..	..	..	..	..	*rrr*		*rrr*	*rrr*	*rrr*	*rrr*	..	*rrr*	..	..	..
B	**Cladocera**	*rr*	*r*	..	*cc*	*rr*	*r*		..	..	..	*r*	..	*r*	..	..	..
7	*Moina dubia*	*r*	*r*	..	*cc*	..	..		..	..	..	*r*	..	*r*	..	..	..
8	*Diaphanosoma paucispinosum* Brehm.	*c*	*c*	..	*cc*	..	*c*		..	..	..	*r*	..	*r*	..	..	..
9	*Daphnia Lumboltzi*	..	..	..	*ccc*	..	..		..	..	..	..	..	..	..	..	..
C	**Rotatoria—**																
10	*Brachionus angularis* Gosse	..	..	..	..	..	*c*		..	..	..	..	..	..	..	..	..
11	„ „ *var bidens* (Plate)	*r*	..	..	..	..	..		..	..	..	..	..	..	..	..	..
12	„ *falcatus* Zach. var B. Weber	..	*r*	*c*	*c*	*rrr*	..		..	*rrr*	..	..	*rrr*	..	..	..	..
13	„ *calyciflorus* Pallas	*r*	..	..	..	..	..		..	..	..	..	..	..	..	..	..
14	„ *forficula* Wierzejski	..	..	..	..	..	..		..	..	..	..	..	..	..	..	*rrr*
15	*Polyarthra platyptera* Ehrenberg	..	..	..	..	..	..		..	..	..	..	..	*c*	*rr*	..	*rrr*
16	*Bdelloidea* (undetermined)	..	..	..	..	..	..		..	..	..	..	..	..	..	..	..
D	**Cercaire—**																
17	*Cercaire furcocergne*	..	*rrr*	..	..	..	..		..	*rrr*	..	..	*rrr*	..	..	..	..
18	*Ergasibus Japonicus* (?)	*rrr*	*rrr*	..	..	..	..		..	..	..	..	..	..	..	..	..

common in 27th April, July, 8th August, September and December, and rare in 8th August and 23rd November.

Cladocera.—Three forms were found of which *Diaphanosoma paucispinosum* Brehm was the most dominant while the other two were subdominant.

Cladocerans were common in 11th April and 25th October, rare in 8th March, 26th May, August and September and very rare in February, 27th April and 13th December.

Rotatoria.—There were seven forms of this group of which *Brachionus falcatus* Zach. *var. B. Weber* was the dominant one while the others were found rare on a few occasions only.

Cercaire.—Two organisms of this group were found and both were found stray on a few occasions only.

Molluscan fauna.—These were not sent for identification, and so the names of the organisms are not listed. But they were seen in large numbers all along the shore in May, June, July and August.

The faunas Copepoda and Cladocera were found in abundance during February to May when *Oscillatoria sp.* was also found at its maximum. But they were found in their minimum from May to August when the molluscs were found in great numbers, the temperature of the water was fluctuating between 29° and 32° C., dissolved oxygen and pH were comparatively low, free CO_2, bicarbonates, total hardness, total and fixed solids, chlorides, organic matter and phosphates were high.

4. Discussion

So, the chief characteristic features of the pond water are : (1) the absence of macrophytic vegetation and scarcity of phyto-plankton, (2) abundance of zoo-plankton (Copepods showing greater seasonal changes than all the plankton animals put together), (3) presence of mussels all along the margin at certain seasons of the year, (4) low oxygen content, (5) slight alkalinity, (6) high organic content, (7) absence of nitrites and nitrates, (8) presence of phosphates, and (9) ammoniacal nitrogen. An attempt has been made below to trace the interrelationship that exists among the several factors mentioned above.

It is well known that food is very important to all kinds of animals, and that when the flora is insufficient or wanting, animal life will be correspondingly poor in any piece of water. But in this pond, it is interesting to note that substances of biological importance such as free carbon dioxide, phosphates, ammoniacal nitrogen and organic matter are present

in fairly large amounts and so they could not have acted as limiting factors to the development of aquatic vegetation and the plankton flora which are very poor or scarce, while the fauna is found in abundance. It is probable therefore that the smaller hours of bright sunshine causes a poor development of the chlorophyll-bearing organisms. This inference appears to be supported by the reaction of the water which is slightly alkaline or almost neutral and by the low oxygen content of the water.

The lack of this important food material for the animals did not prevent them from growing in large numbers throughout the year. Their abundance needs explanation. In the first place, the chief food of the zoo-plankton is very probably the nano-plankton organisms which ordinarily escape the net and are reported to be present in abundance in all fresh waters. Woltereck[19] (cited by Krogh[12]) has observed rich nano-plankton flora in the Lunzer Lake, where it made up the main food of the Cladocera. In the pond under investigation Copepods dominate the catches and it is therefore quite likely that they depend upon the nano-plankton in the pond water for their food.

Secondly, according to Carpenter[6] animal life is richest in waters of slight alkalinity and seldom occurs at all below pH 4·7 or above 8·5. The pH range of this pond water is only between 7·6 and 7·8 indicating very slight alkalinity. It is therefore very probable that the slight alkaline reaction of the water is one of the factors favouring the prolific growth of the zoo-plankton.

But the actual pH of the water alone cannot be considered as a single isolated factor of biological significance, as it is the resultant of several factors, each of which may also exercise a great ecological influence. Among the several physico-chemical factors which affect the hydrogen-ion concentration of water may be mentioned the temperature of the water, biological effects due to respiration by plants and animals, photosynthesis by plants, the removal of carbonates by shell-forming organisms, the sources of carbon dioxide and the availability of a supply of calcium carbonate.

Considering briefly each of these factors, it may be seen that the range of temperature of the water is between 24° C. and 32° C. ; the respiratory activities are greater than photosynthetic activities, as is evident from the low figures of dissolved oxygen, high content of free CO_2 and the slight alkalinity of the water. The existence of mussels indicates that a good portion of the lime content as calcium carbonate is removed from the water but is returned to it after their death in the form of bicarbonate, due to CO_2 resulting from the bacterial decomposition of the excessive amount

of organic matter. But the fact that the pH of the water is not considerably altered at any time of the year, in spite of the withdrawal of calcium carbonate by the mussels for their shell formation would seem to show that there is another source of supply. It is the spring water from the well with which the pond is connected, which probably replenishes the loss, so that the calcium-bicarbonate—carbonate equilibrium is not radically altered. So the reaction of the water remains always slightly alkaline and the pH fluctuates within very narrow limits.

5. *Summary*

1. The seasonal changes for a year in the physico-chemical variables of a garden pond containing abundant zoo-plankton are traced. The important features of the pond water are its low oxygen content, slight alkalinity, high organic content, scarcity of phyto-plankton and abundance of zoo-plankton and mussels.

2. The dominant zoo-plankton consisted of Copepods.

3. Interrelationship existing between the environmental conditions in the pond on the one hand and the animals on the other is discussed.

Acknowldgments

The author wishes to express his deep sense of gratitude to Dr. P. Chappuis of the University of Cluj for help in working out the periodicities of the several groups of zoo-plankton generally, and to the other specialists Dr. F. Kiefer for Copepods, Dr. V. Brehm for Cladocera, Dr. J. Hauer for Rotatoria and Dr. Dolfuss for Cercairæ and to Dr. M. O. P. Iyengar of the University of Madras for help in the identification of the phyto-plankton.

His thanks are also due to Rao Bahadur Dr. C. S. Govinda Pillay and to Dr. P. Sadasivan for their interest in the work.

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INDIAN SILICIFIED PLANTS*

2

Enigmocarpon Parijai, a Silicified Fruit from the Deccan, with a Review of the Fossil History of the Lythraceæ.

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Received November 18, 1942

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Introduction

THE generic name *Enigmocarpon* was given by me to some silicified fruits found in one of the basal members of the Deccan Intertrappean Series exposed at Mohgaon Kalan, in the Chhindwara District, C.P. (Text-Fig. 1). This important and richly fossiliferous locality was discovered about twelve years ago by Professor K. P. Rode of Waltair, then Assistant Professor of Geology at the Benares Hindu University, who has himself made interesting contributions to our knowledge of the Intertrappean flora. In a note published in 1933 Rode announced the discovery of a number of petrified angiosperm fruits at this locality, and on that occasion he also gave, *inter alia*, a brief description of the species which forms the subject of the present paper (Rode, 1933, pp. 171–72). The fruit was correctly described as an

* The first paper in this series appeared in Vol. XIV, No. 6 (1941).

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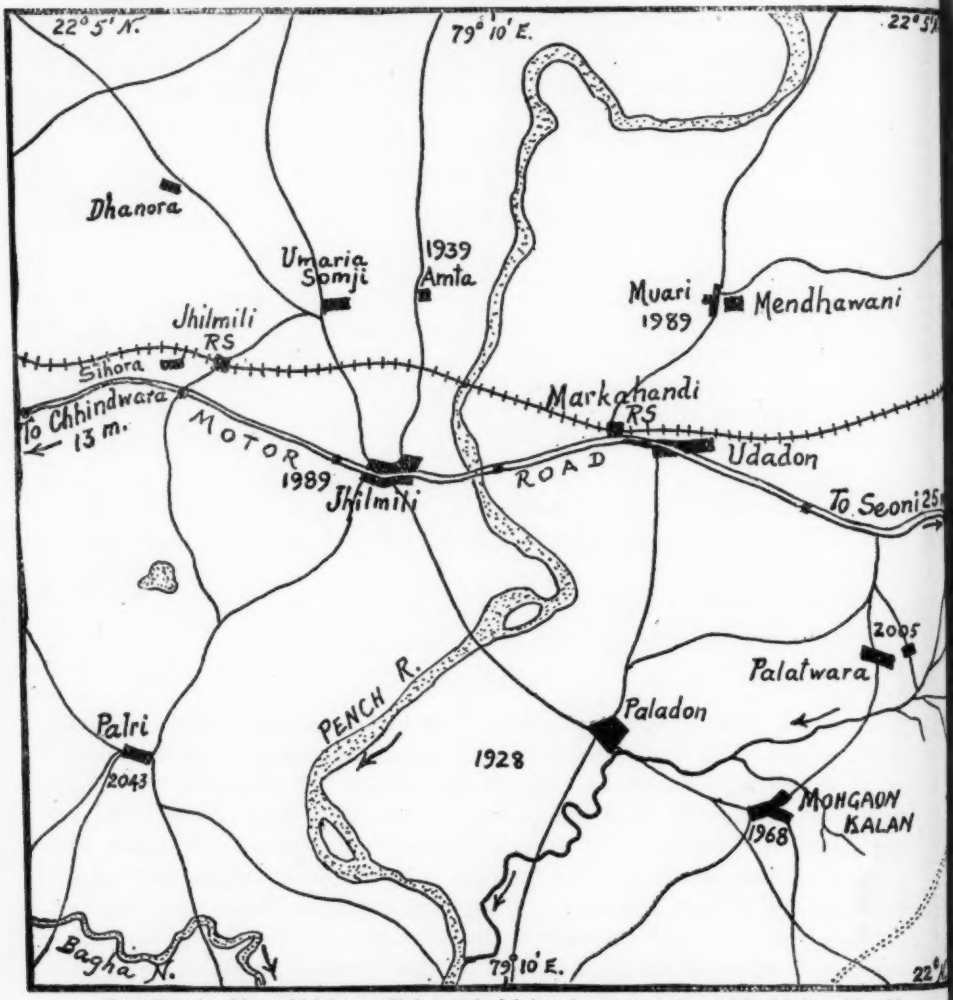
8-chambered loculicidal capsule with numerous ovules attached to a stout axile placenta. It was compared in a general way (without commitment as to affinity) with the genus *Cucumites* of Bowerbank (1840). No name was assigned to the fossil and no figures were given.



TEXT-FIG. 1. Map of Mohgaon Kalan and vicinity, based on Survey of India sheet No. 55 N/4. Scale 1″ = 1 mile. The figures indicate heights in feet above sea-level.

In the meantime I had paid a visit to the locality in January 1931, when a quantity of further material of this species (and of other interesting types)

was collected. Brief descriptions with photographs were published partly on the basis of this material, partly on specimens kindly made over to me by Professor Rode (Sahni, 1937, 1938, 1940). During the past 10 or 12 years repeated visits by Professor Rode, Mr. V. B. Shukla and myself have shown that this fruit is one of the commonest fossils at this prolific locality. So far as I know it has not been found anywhere else, and we have only one species, named after my friend Professor Parija of Cuttack, in whose company my first visit was made.

My best thanks are due to Professor Rode for the material he generously placed at my disposal. To Mr. V. B. Shukla I owe two peel sections made by Dr. A. R. Rao which show well the possibilities of this technique in the investigation of silicified remains. Mr. Boshi Sen very kindly gave me laboratory facilities at Almora for which it is a pleasure to record my thanks to him. The photographs here reproduced were prepared by Dr. R. V. Sitholey whose able assistance I always value.

Suspecting that, like some other Deccan fossils I have described elsewhere, these fruits were preserved in volcanic ash deposited on stagnant water, I sent the sections shown in Photos. 18 and 24 to Professor Rode for a petrological examination. He writes (31–7–1942) " The matrix appears to be all chertified tuff..... chiefly composed of minute fragments of brownish, opaque to translucent glass cemented together in secondary silica." The fruits, as the photographs show, are beautifully preserved with usually little or no shrinkage of tissues : evidently they were buried in the submerged condition, being overwhelmed by the ash soon after they had reached the water. But mixed up with them in the same matrix are innumerable dark specks and shreds of vegetable matter, usually with hardly any recognizable structure. These were apparently derived from exposed plants charred with heat and blown to smithereens which settled down on the water with the volcanic ash. A few sections of charred leaves appear as thick black streaks but with the cells of the palisade and spongy mesophyll, and in the midribs and veins, still clearly recognisable as silhouettes.

Description

Genus *Enigmocarpon* Sahni, 1934

A genus of confirmed aquatic or marsh plants with the fruit and seed adapted for aquatic dispersal. Fruit a dry multilocular capsule with axile placentation and loculicidal dehiscence, the septa coming off with the valves. Calyx (?) *persistent. Seeds numerous, anatropous, attached horizontally in two vertical rows in each loculus. Integument* (? *single*) *multilayered, rich in fibrous tissue, with a great development of spongy tissue in the much enlarged raphe. The*

raphe carries in the median plane a vascular bundle which at the chalaza expands into a pad of tracheids directly underlying a hypostase (a pad of thick-walled cells forming the nucellar base). The epidermis of the nucellus persists as a bag, with its hardened conical apex drawn out into a long narrow process. Embryo straight; endosperm absent.

Enigmocarpon Parijai Sahni

1933 (*no name*) K. P. Rode :		*Curr. Sci.* II (5), 171–2 (no figs.).
1934 *Enigmocarpon Parijai* Sahni :		*Proc. 21st Ind. Sci. Congr.* (Bombay), 317 (no figs.)
1937	,, ,,	*Proc. Nat. Ac. Sci. India*, VII (3), 168, figs. 8–15.
1938	,, ,,	*Proc. 25th Ind. Sci. Congr.* (Calcutta), 162, Pl. 2, fig. 14.
1940	,, ,,	*Proc. 27th Ind. Sci. Congr.* (Madras), 15, fig. 14.

DIAGNOSIS.—*Capsule ellipsoid* 7-9 (*usually* 8)*-locular*, ca. 18 *mm. long*, 14 *broad, attached on a long slender stalk. Placenta cylindrical*, ca. 3 *mm. thick, with a central lysigenous canal and a peripheral lacunar zone continuous with the lacunar tissue of the septa. Fruit wall externally smooth*, 2–3 *mm. thick, markedly spongy. Seeds obovate—triangular*, ca. 3 *mm. long, about* 18 *per loculus, packed horizontally, back to back in two alternating rows, more or less obpyramidal by mutual compression, their anterior sides moulded by the smooth rounded interior of the loculus. Chalaza more or less obliquely placed; micropyle curved towards the short thick funicle. Raphe as thick as the seed-body or thicker, much expanded distally, partially embracing the seed-body. Epidermal cells of integument polygonal with sinuous side walls, the outer wall of each cell having a central hyaline papilla. Below the epidermis everywhere are several layers of fibrous cells placed longitudinally. Seed-cavity lined with very narrow elongated thick-walled cells placed lengthwise. Spongy tissue of raphe consists of thin-walled spherical cells. The supply bundle from the funicle, enclosed in a raphe-canal lined with fibres, at first runs close to the posterior surface of the raphe, then bends in an ascending sigmoid curve in the median plane, through the spongy tissue, to reach the obliquely placed chalazal pad of tracheids, itself enclosed in a jacket of fibres. Hypostase crescent-shaped in median section, of small thick-walled polygonal cells, its periphery continued into the persistent nucellar epidermis, the latter of larger polygonal cells which distally are placed in longitudinal rows converging to an indurated conical cap ("epistase") which is produced into a style-like process* ca. ·25 *mm. long. Cotyledons slightly concave adaxially, merging below into the radicle.*

Locality.—Mohgaon Kalan (22° 1′N.; 79° 11′ E.), about 18 miles east of Chhindwara, C.P. and two miles south of the Chhindwara-Seoni motor road. (*N.B.*—Several villages in this district bear the name Mohgaon, but there is only one Mohgaon *Kalan.*)

Horizon.—Basal part of the Deccan Intertrappean Series, about 100-130 feet above the Archæan Gneiss, which directly underlies the lowermost trap flow in this area (see Rode's Sketch of the Geology of the Chhindwara District, in Sahni and Rode, 1937, pp. 171–74).

Geological Age.—Early Tertiary, probably Eocene.

Figured Specimens and Sections.—In the Sahni Collection. Specimens were first collected by Dr. K. P. Rode (1929–30), later by the author and Professor P. Parija (1931); recently (1941, 1942) by the author, Mr. V. B. Shukla and others. All the figured specimens and sections have now been placed in the Sahni Collection and should be regarded as syntypes.

General features

About 50 specimens of the fruit have been examined and of these at least a dozen have been made into thin sections. It would be difficult to designate any one of these as the type-specimen, because several of them have contributed materially to our knowledge of the structure and its variations. The most important specimens are shown in Photos. 1, 6, 16, 18, 23, 24, 29, 30.

Photo. 1 shows two well preserved fruits exposed on the freshly broken surface of a piece of black chert. One of them is fractured longitudinally and shows well the thick fruit wall enclosing the numerous ovules placed horizontally on a stout central axis. The same two fruits, cut in a slightly different plane, are seen as thin sections in Photos. 21, 22. In Photos. 2, 3 are other specimens exposed on the naturally fractured and weathered surface of the rock. Photo. 4 shows the concave impressions left by half-a-dozen fruits of which no other trace remains. The series of pits formed by the distal ends of the rows of seeds are in one case surrounded by a border representing the thick fruit wall. The capsule is sometimes seen already dehisced into valves (Photo. 9). The elongated seeds, often prominent owing to their whitish colour, are commonly found scattered in the rock matrix where they are seen cut in various planes. The ellipsoid fruit varies in length from about 15 to 18 mm.; the widest cross-section is 16 mm. The external surface is smooth, except for the slight grooves marking the positions of the septa. Photo. 13 suggests that the base was slightly invaginated in the centre and this is confirmed by the only stalked specimen I have seen (Photos. 7, 8). From Photo. 9 it appears that at dehiscence the converging valve-tips turned slightly upwards

to form a depressed cone ; the elongated form of the same specimen, seen longitudinally fractured in Photo. 10, is probably due to lateral compression.

The stalk is slender; the structure is not at all well preserved in the only section available, which is longitudinal.

As a rule all the 8 loculi are fertile and equally developed. Photo. 13 shows the only 9-locular specimen I have seen; 7-locular fruits are also rare.

Anatomy of the fruit

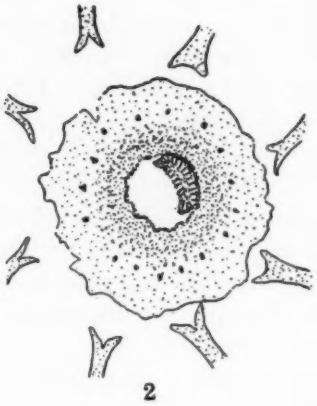
The placentation, mode of dehiscence and other features are well seen in Photos. 18, 23, 24. The axile placenta, 2–3 mm. thick, is traversed by an axial canal, a lysigenous cavity originally occupied by a delicate tissue of which traces are preserved in some sections (Photos. 18, 24, 26; Text-Figs. 2, 3). In Photo. 18 (*cf.* Text-Fig. 2) a small sausage-shaped patch of tissue is seen applied to the upper right-hand side of the canal. This patch includes the crushed central tissue with a surrounding narrow ring of vascular bundles now pressed and flattened out to one side (Text-Fig. 2). The same central tissue and its surrounding vascular ring are seen undisturbed in the peel section shown in Photo. 26, the elliptical form here being due to the oblique plane of section. Round the vascular ring lies a compact zone of parenchyma forming an inner cortex; this is covered by a wide outer cortex rich in air spaces from which the radial septa, similarly composed of lacunar tissue, easily break away. The outer cortex contains another ring of bundles, of which sixteen can be counted in the section shown in Photo. 18, Text-Fig. 2. This ring of sixteen strands evidently is the source of the ovular supply bundles, there being two vertical rows of ovules in each loculus.

The septa do not reveal any vascular traces but in the peripheral parts of the carpel valves these are again frequent, showing that the fruit wall was supplied directly from below, not through the septa.

The epidermis of the fruit is a layer of relatively small, somewhat flattened isodiametric cells, covering about four layers of very thick-walled slightly elongated cells, below which there are a few layers of thin-walled compact parenchyma. The inner lining of the loculi is a smooth epidermis-like layer. The whole of the remaining thickness of the valves and of the septa is composed of markedly spongy tissue, the cells being elongated, often slightly branched and so arranged as to leave large inter-spaces (Photo. 21).

The loculicidal sutures are simple radial fractures, along pre-determined lines where the fruit wall is slightly thinner. From the middle of each valve the relatively thin septum projects inwards as far as the placental column, to which it is attached by a slightly expanded margin, in section appearing

split like a swallow's tail. This attachment is, however, not a firm one, for at the time of dehiscence the septum comes off with its corresponding valve, to which it is permanently fixed by a much expanded distal margin.



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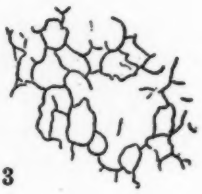

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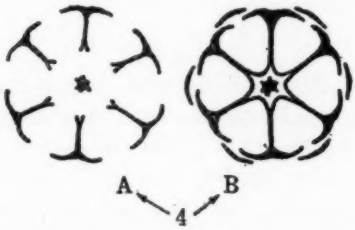

A B

4

TEXT-FIGS. 2–4.—Fig. 2. Simplified camera-lucida sketch (diagrammatic) of placenta from the fruit shown in Photo. 18 (*cf.* also Photo. 26). Compact inner cortex densely dotted, loose outer cortex, with 16 vascular bundles, sparsely dotted. The septa, here broken off from the axis, show their bifurcated inner margins (as also in Photo. 24). ×12. Fig. 3. Remnants of the delicate central parenchyma from the placenta shown in Photo. 26. Peel section by Dr. A. R. Rao. Camera-lucida sketch. ×105. Fig. 4. *Lagerstroemia indica.* A, section across the middle of the fruit, B, across the lower half. See text. Diagrammatic. ×*ca.* 2½.

The longitudinally split inner margins of the septa deserve some further notice, for they appear to me to suggest an interesting detail in the mode of dehiscence which may be comparable with what I have seen in the fruit of a modern *Lagerstroemia.* In this genus, too, a section across the middle of the fruit (Text-Fig. 4 A) shows the inner margins of the septa swallow-tailed as in our fossil, but in the lower half of the fruit (Text-Fig. 4 B) the two divergent limbs of each septum are fused laterally with those of the septa to right and left so as to form, all together, a small star-shaped chamber round the

shrivelled column of the placenta projecting freely from the centre. These facts suggest that a cross-section through the lower part of the *Enigmocarpon* may also reveal a similar condition. Unfortunately I have no section passing through this region of the fruit, but the point ought to be looked into.

As nearly all the fruits examined had already dehisced, the number of seeds actually seen attached to the placenta is small. But there is no room for doubt that all the seeds were attached in an axile manner. This is obvious at a glance from the cross-section shown in Photos. 18, 24. The funicles are extremely short, so that the seeds may be described as sessile or sub-sessile. They are anatropous and the embryo (found only in a few) is straight.

In each loculus the seeds are about 18 in number and closely packed, placed horizontally in two alternating rows, so that they are flattened on their contiguous sides. But as they are of a fairly large size, even a slighfly oblique cross-section through a fruit may give the impression, at least locally, that the rows are opposite (*cf.* Photo. 18).

The lacunar nature of the placenta, septa and carpel valves makes the fruit eminently fitted for transport by water. As we shall now see, the seeds are equally well adapted for aquatic dispersal.

Anatomy of the seed

Of the several peculiar features of the seed the most striking are (i) its general form, the obliquely placed chalaza and curved micropyle ; (ii) the enormously enlarged raphe, its great mass of spongy tissue and the characteristically curved vascular bundle, expanding into a tracheidal pad at the chalaza ; (iii) the persistent nucellus with its hypostase, epidermis and conical apex ("epistase") produced into a long bristle-like process ; (iv) the thick integument, rich in fibrous tissue and covered by a papillate epidermis.

The outline sketches in Text-Figs. 6 to 15* are from sections cut in the various planes marked in the accompanying index figure. All these sections are also shown in the photographs. Text-Fig. 5 was made up from a number of sections, the form and size of the embryo being inferred only from a few transverse and oblique sections.

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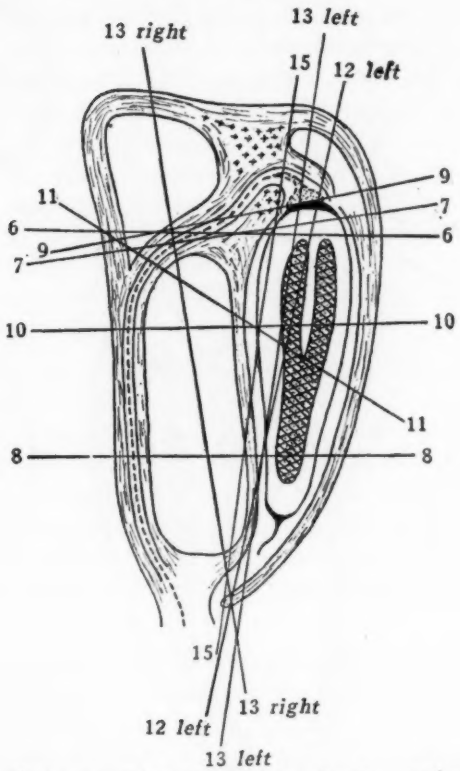
* In drawing these and other camera-lucida sketches of the seeds an attempt has been made to combine simplicity with a reasonable degree of accuracy. Some of the sections being thick, the same object appears slightly different at different levels of focus. The planes of section marked in the Index Figure must be regarded only as approximations ; they were only inferred from the form, size and position of the structures revealed in them ; moreover, several of the planes do not lie normally to the plane of the paper. Some apparent discrepancies must be due partly to variations in the form of the seeds, partly also to shrinkage during fossilisation.

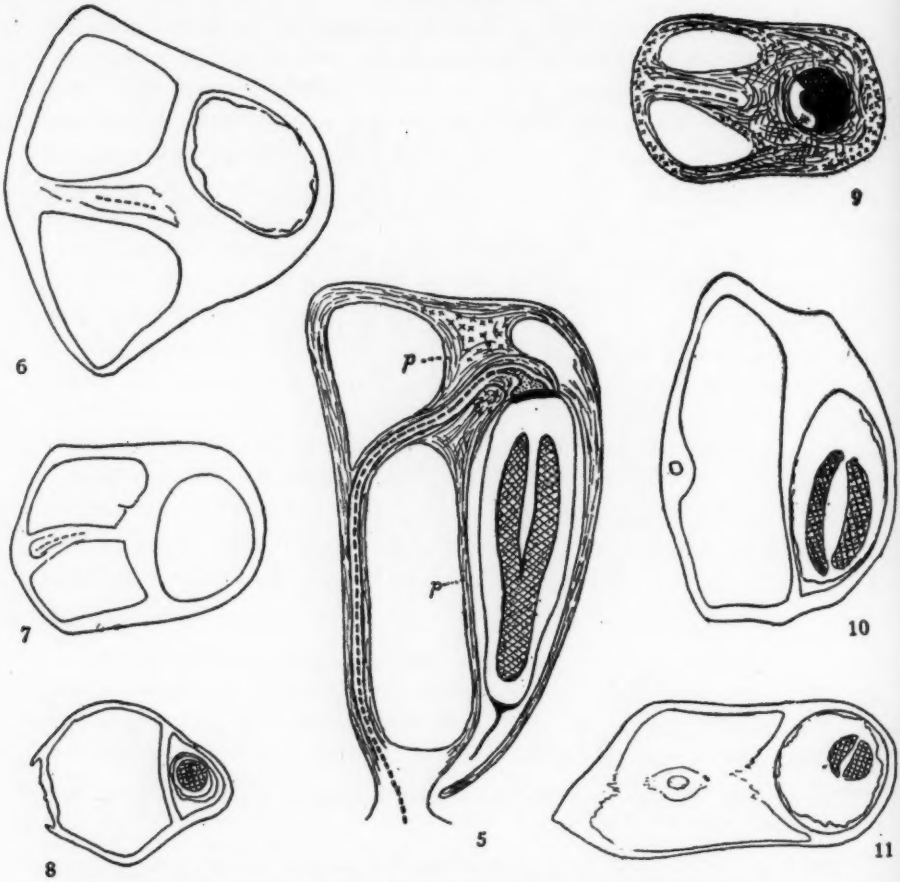


INDEX FIGURE. Showing approximately the planes of section of Text-Figs. 6–15. See footnote, page 34.

Photos. 18, 24 show at a glance that the peculiar form of the seeds as seen in longitudinal section is imparted to them by the way they lie pressed against each other back to back and hemmed in anteriorly by the curved walls of the loculus. The varying form of the cross-section of the seed is well understood from Photos. 16, 23 which show the fruit cut tangentially. An inspection of these photographs, and a comparison of the sketches in Text-Figs. 5–11 by reference to the index figure, should make any long description unnecessary.

Well over half the volume of the seed is taken up by the swollen raphe, which is specially expanded at the distal end.

Throughout its course the vascular bundle is enclosed in a sheath of longitudinal fibres, at least three layers thick, which in all but the thinnest sections appears as a dark band, like the fibrous zone of the integument.



TEXT-FIGS. 5–11.—Fig. 5. Sagittal section of ripe seed, reconstructed from several sections. Vascular bundle shown as a broken line; chalazal pad of tracheids dotted; hypostase and epistase solid black; embryo cross-hatched; longitudinally cut fibres of integument shown as lines, those transversely cut as crosses. Diagrammatic. ×*ca.* 27. Figs. 6–11. Cross-sections of seeds (more or less oblique) along planes approximately shown in the Index Figure. Conventional shading (where shown) as in Text-Fig. 5. Based upon camera-lucida sketches from actual sections which are all shown in the photographs (*cf.* Photos. 16, 23). Further explanation in text. All ×27.

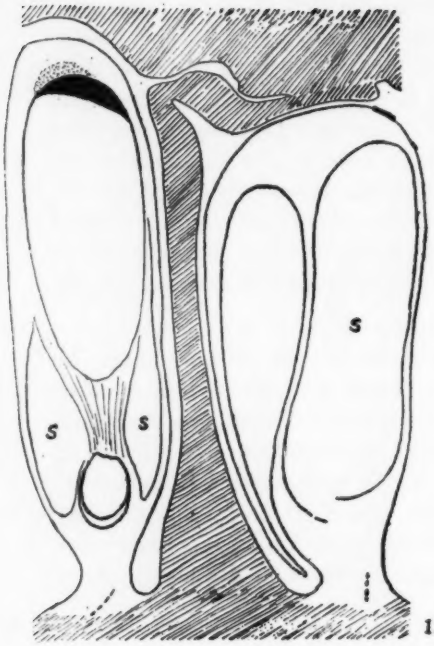
Where the bundle runs vertically, close to the posterior middle line of the raphe, the raphe canal is fused to the fibrous zone of the integument. Where it ascends in a sigmoid curve towards the chalaza it cuts obliquely through the spongy tissue of the raphe (Text-Fig. 5), appearing (as seen in a median longitudinal section) to divide it into two very unequal parts.

Cross or oblique sections through this part of the seed show the raphe as if partitioned into equal right and left halves (Text-Figs. 6, 7, 9), a fact which at first conveys the deceptive appearance of a curved embryo with two cotyledons bent parallel to the radicle. In the distal part of its course the raphe canal has to pass through a large mass of sclerenchyma lying below and around the chalaza, where the fibres seem at first to form an almost hopelessly confused tangle. The vascular bundle, always enclosed in its fibrous sheath, and never giving off any branches, passes through this tangled mass and then swerves rather sharply downwards into the obliquely placed chalaza, where it expands suddenly into a pad of short scalariform tracheids recalling transfusion tissue.

The somewhat complicated situation in this region will, I hope, be tolerably clear from the photographs and simplified camera-lucida sketches of sections cut in different planes. The impossibility of preparing orientated sections through individual seeds makes it difficult to follow all the details of structure, but this is largely compensated by the large number of seeds that we find cut in a single fruit, and by the fact that their position within the fruit is not entirely unknown to us. The planes marked on the Index Figure may therefore be taken as fairly good approximations to the actual planes of section.

In the sketches the longitudinally cut fibres are shown as lines, those transversely cut as crosses ; the vascular tract is a thick broken line but where it expands or is seen cut across, it is shown as a dotted patch ; the hypostase and epistase are solid black, the embryo cross-hatched ; portions of the carpels or placenta are obliquely shaded. The fibres, however, have been omitted from some of the figures and from portions of others, for the sake of simplicity and clarity.

The rather complex structure becomes easier to follow if we remember (i) that everywhere the subepidermal fibres of the integument run lengthwise, parallel to the epidermis, (ii) that the fibres of the raphe canal run parallel to its course, following also the features of the tracheidal pad in the same manner, (iii) that in the region of the chalaza the fibrous sheath forming the raphe canal is specially thick and (iv) that in this region there is an extra girdle of fibres (see Text-Fig. 15) which passes like a hoop round the raphe canal *transversely*, that is, in a plane at right angles to its course. This extra girdle forms the bulk of the great mass of sclerenchyma below and around the chalaza ; its distal loop is much thicker than the proximal which has to pass through the narrow space between the seed body and the last curve of the raphe canal. The form and position of this girdle will be best understood by comparing



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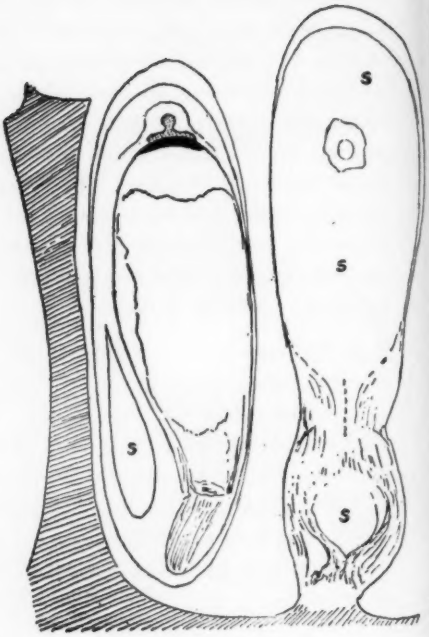

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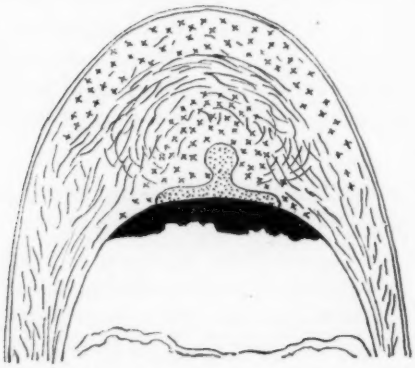

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TEXT-FIGS. 12–15.—Figs. 12–13. Longitudinal sections of seeds in planes approximately shown in the Index Figure. Carpellary tissues obliquely shaded; other conventions as before; *s*, spongy tissue. Based upon camera-lucida sketches of actual sections shown in Photo. 6. The seed in Text-Fig. 12 (right) is cut approximately in the sagittal plane. ×27. Fig. 14. Chalazal end of seed shown in Fig. 13 left. ×78. Fig. 15. Longitudinal section of seed, cut approximately in the plane shown in the Index Figure but not normally to the plane of the paper. ×27.

Text-Fig. 5 with Text Fig. 15 which shows a section cut roughly in the plane of the girdle. In Text-Fig. 14 the section is parallel to the latter, but the plane of section being nearer the chalaza the proximal loop of the girdle is cut off by the tracheidal pad. On its anterior and posterior faces the girdle is again covered by fibres which lie longitudinally between it and the spongy tissue of the raphe (*p* in Text-Fig. 5). These fibres merge distally into the fibrous sheath of the integument and proximally are continued into the relatively thin fibrous partition (the lower *p*) separating the nucellus from the spongy tissue of the raphe.

So far as I have been able to ascertain, there was only a single, though multi-layered, integument but the structure is not very clear in the critical region of the micropyle. It is possible that the lining of very narrow thick-walled cells (*i* in Photo. 19) represents a closely appressed inner integument, but it is equally possible that this is only the innermost layer of a single thick integument. In one or two seeds (*e.g.*, see Photo. 29 and Text-Fig. 23) we see round the bristle-like process of the epistase certain dark patches which may possibly be the crushed remains of an inner integument, but there is no evidence of preserved cell structure, and the patches may not be of organic nature at all. Considering the affinities of the fossil, which are now known to be with the Lythraceæ, one would expect to find two integuments, but in the absence of clearer evidence the question must be left undecided till better preserved material is discovered.

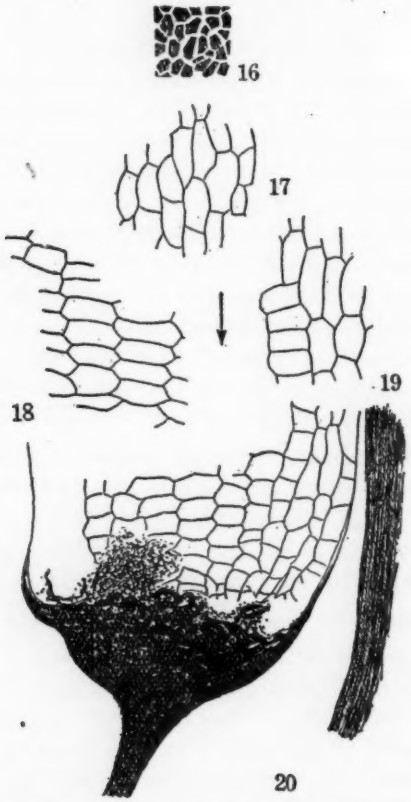
The epidermis all over the seed-coat consists of a single layer of slightly thickened and sinuous-walled cells, each provided with a central hyaline papilla (Text-Figs. 27, 28, Photos. 11, 19, 28). The part of the exposed cell wall forming the papilla was left thin: very probably the papillæ helped in the imbibition of water by the germinating seed.

Netolitzky (1926, p. 235) mentions the occurrence of simple epidermal papillæ on the seed-coat of the modern Lythraceous genera *Nesæa* and *Heimia*, but he does not figure them, and I have been unable to obtain seeds of these plants for comparison. There is no evidence in *Enigmocarpon* of the peculiar "internal hairs", described by several botanists in *Lythrum*, *Peplis*, *Ammannia* and *Cuphea* (for references see Netolitzky, pp. 235–236 ; also Haberlandt, 1914, pp. 209–10).

This brief description sufficiently stresses the great development of the raphe in the ovule of *Enigmocarpon*. In comparison the essential part of the ovule is both shorter and thinner. The nucellus was free right down to its base. The only parts of it preserved in the fossil are those, evidently, that persisted in life up to the seed stage, being cutinised or otherwise indurated.

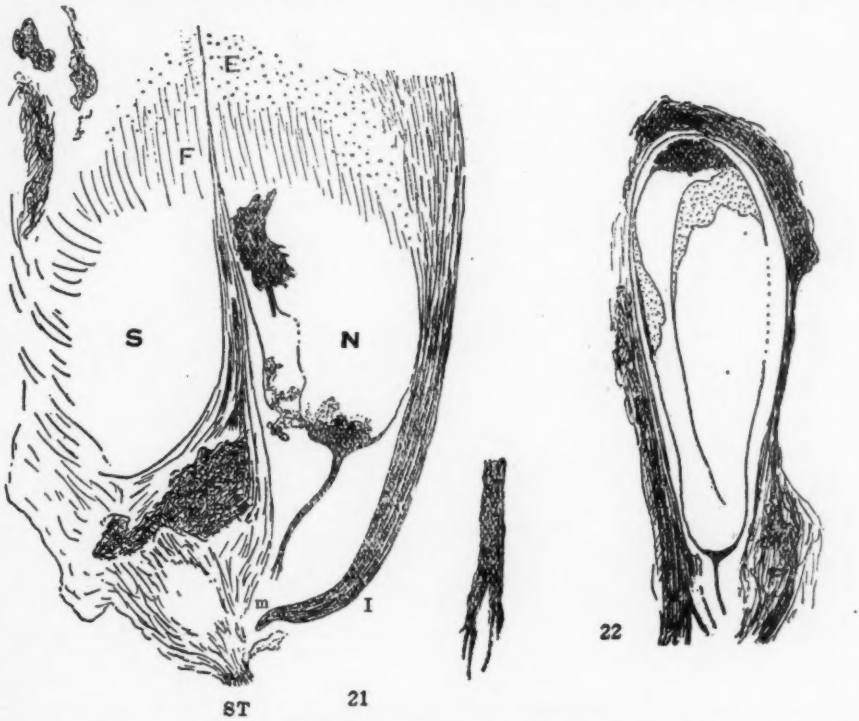
These are (i) the hypostase, (ii) the bottle-shaped bag of nucellar epidermis (or perhaps it is only the cuticular membrane with the cell outlines impressed upon it) and (iii) the epistase, a little conical cap with its apex drawn out into a gently curved bristle as much as a quarter of a millimetre long, which lies in the micropylar canal.

The hypostase is seated directly upon the chalazal pad of tracheids. It is shaped like a very shallow saucer thicker in the middle than elsewhere,

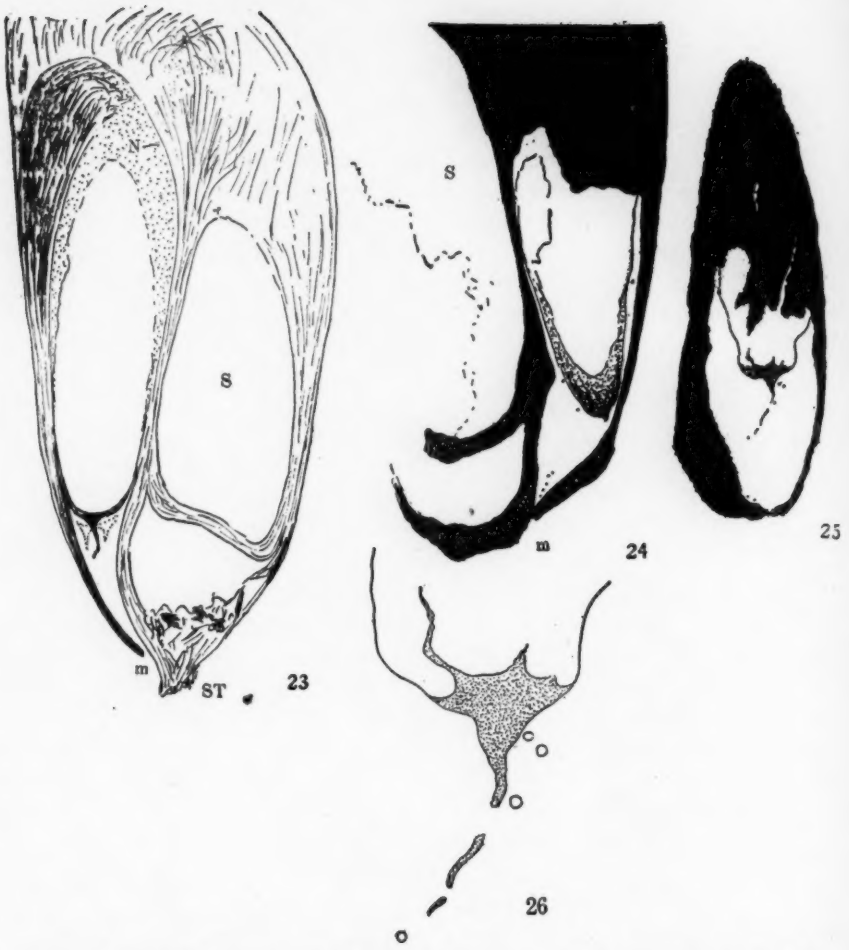


TEXT-FIGS. 16–20.—Fig. 16. A few cells from the hypostase, showing the thick walls and dark lumina. ×262. Fig. 17. Cells from the nucellar epidermis (lower half of a seed). The cells are elongated parallel to the seed axis. ×262. Figs. 18–19. The same, from the middle region of the seed in Photo. 29, showing tendency for arrangement in longitudinal rows. The arrow indicates the axis of the seed. ×262. Fig. 20. Distal part of the nucellus of the same seed, showing part of nucellar epidermis, and the "epistase"; the greater part of the bristle-like tip is omitted. Only a part of the thickness of the integument is shown (to the right). See Text-Fig. 21. ×262.

so that (in well-preserved specimens) the section is like a crescent (Text-Figs. 12, 13) ; it is made up of small polygonal cells of which the thick pitted walls appear white and the cavities dark (Text-Fig. 16), so that the hypostase as a whole appears as a black concave disc. The thin margin of the hypostase is continued directly into the nucellar epidermis of which the similarly polygonal cells are, however, larger and not so thick-walled (Text-Fig. 17). In places these cells are seen transversely elongated and arranged in neat longitudinal rows (Text-Fig. 18, 19, 20) ; as the rows converge to the apex the cells become smaller, till their outlines disappear in the black indurated cone-like apex. The tip of the bristle is sometimes seen frayed out (Text-Fig. 21). At first it might appear that this membranous bag with its long



TEXT-FIGS. 21 & 22.—Fig. 21. Oblique longitudinal section (nearly median) of the same seed as in Text-Fig. 20, showing *e*, epidermis of integument ; *f*, fibrous layer of integument ; *n*, nucellus ; *s*, spongy tissue of raphe ; *m*, micropyle ; *i*, integument ; *st*, funicle. ×78. To the right the frayed out tip of the nucellar process is shown × 394. Compare Photo. 29. Fig. 22. Longitudinal section of another seed (compare Photo. 30). Hypostase and epistase solid black, nucellar membrane shown dotted where seen in surface view, as a line where seen in section ; integument densely shaded with lines. Further explanation in text. ×34.



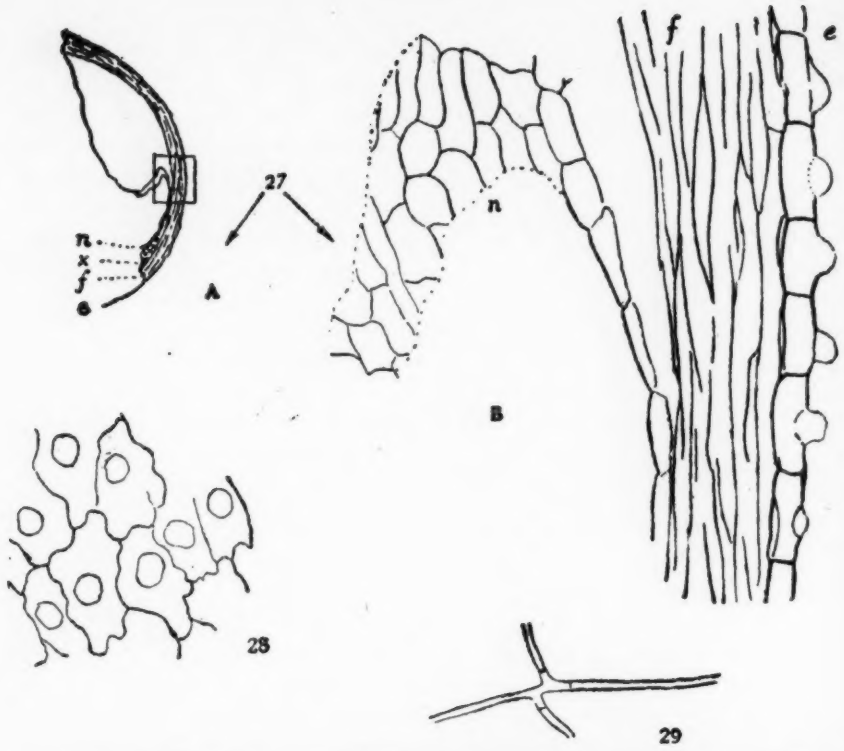
TEXT-FIGS. 23–26.—Fig. 23. Longitudinal section of another seed, nearly median, from the section shown in Photo. 18. *n*, nucellus (see Photo. 20); *s*, spongy tissue of raphe; *m*, micropyle; *st*, funicle. Round the nucellar process a dark crushed patch is present, which here is shown by a dotted outline. Further explanation in text. ×39. Fig. 24. Tangential longitudinal section (from a "peel" made by Dr. A. R. Rao). Nucellus shown dotted, integument solid black; *s*, spongy tissue of raphe; *m*, micropyle. Inside the micropylar opening a row of cells simulating pollen grains; two or three similar cells lie round the nucellus. Of the bristle-like nucellar process only the very base is seen. ×39. Fig. 25. A similar section, from another seed in the same "peel". Near the nucellar process, which is here seen broken in three pieces, are several free-lying cells similar to those in Fig. 24. ×*ca.* 39. Text-Fig. 26. The nucellar apex and the pollen-like cells from Fig. 25. ×*ca.* 140.

beak is an inner integument. Dr. P. Maheshwari, who has seen my photographs (but not the sections) inclines to this view. But the cutinised nucellar membrane is by no means unknown to persist in angiosperms. In *Cuphea petiolata* Mauritzon (1934, p. 13) even describes about 10 layers of the nucellus becoming converted into an epistase-like cap.

That the nucellus is completely free from the integument is shown by the fact that it frequently lies as a loose bag, shrunk away from the integument, although more commonly it is seen closely applied to it, at least in the broader part of the seed. Photo. 30 should be compared with Text-Fig. 22. As explained in the legend, the nucellar membrane on the left has been thrown into a longitudinal fold and is therefore seen cut along two lines. The outer limb of the fold is more or less closely applied to the integument but at the chalazal end it is clearly seen joining the edge of the hypostase. The inner limb looks as if it has been torn loose from the hypostase, except on the right where it is joined to it in symmetry with the junction on the left. The basal part of the nucellar membrane is seen in surface view, like some portions of the outer limb of the fold on the left.

The seed shown in Photo. 29 and Text-Fig. 21 has been sectioned in an obliquely longitudinal plane. The chalazal end has been cut off. From the region *e*, where the little white dots mark the epidermal papillæ of the integument, the plane of section transgresses by turn to deeper and deeper parts : first to *f*, the fibrous zone of the integument, then to *n* the nucellar epidermis, here seen obliquely in surface view, finally to the nucellar tip and micropyle. Similarly, in the raphe we have *e*, *f* and *s* (spongy tissue), lastly the funicle (*st*). Another seed, shown in Text-Fig. 23, has been cut more nearly in the median plane.

In two of the ovules (Text-Figs. 24–26) there are, in the micropylar chamber, a number of isolated spherical or ellipsoid cells which, had we been dealing with a gymnospermous type, would at once have been accepted as pollen grains. A few of them lie near the nucellar cap, others round the beak, others again form an irregular row in the micropylar canal. It is by no means claimed that they actually are pollen grains, but the occurrence of free-lying cells in this region is worthy of note. They have a definite cell wall round them and a granular interior. They do not appear to be fungus spores, nor is there any sign of a mycelium in the vicinity. For the present it is best to leave them at that. But I ought to add that in another seed, not in the same fruit as these problematic cells, traces of a septate fungal mycelium were found (Text-Fig. 29).



TEXT-FIGS. 27–29.—**Fig. 27.** *A*, Part of the seed marked ⊙ in Photo. 6, showing fibrous ntegument and shrunken nucellar membrane. At *f* the fibres are longitudinally placed, at × transversely cut. The region enclosed in the rectangle is further enlarged in *B*, to show details of *n*, nucellar membrane; *f*, zone of longitudinal fibres of integument; *e*, epidermis of integument, with papillæ. *A*, ×27; *B*, ×394. **Fig. 28.** Surface view of epidermis of integument (*cf.* Photo. 11). ×394. **Fig. 29.** Fungal hyphæ from near the seed marked * in Photo. 6. ×394.

In a few seeds the remains of an embryo are seen, but the structure is not so well preserved as to enable one to describe it in any detail. The embryo must have been straight. In Photo. 28 and Text-Fig. 10 the two cotyledons are seen facing each other by their slightly concave adaxial faces. No vascular bundles can be made out but this may be due to the preservation. In Text-Fig. 11, where the section passes through the base of the cotyledons, it seems as if the cotyledons were stalked, the apposed semicircular cross-sections of the stalks together forming a circle which no doubt merged into the radicle. I have not seen any sections through the plumule, but several show the radicle as a cylindrical organ about ·2 mm. thick. The form and size of

the embryo as shown in Text-Fig. 5 is only inferred from a few cross and oblique sections.

No trace of an endosperm is visible in any of the seeds. Between the embryo and the nucellar membrane there is usually a fairly large space which must have once been occupied partly by the nucellus, partly by the endosperm. This space probably indicates the digestive activity of the endosperm at the expense of the nucellus, and (later) of the embryo at the expense of the endosperm. It appears that the whole of the endosperm was absorbed : the preservation of the seeds is so good that, had any traces of the endosperm been left at this stage of development, they would have been preserved. We may therefore conclude that the seeds were exalbuminous. Of course, it might on the other hand be argued that an endosperm may have been present and that it was not preserved because of its contained food reserves, which may have rendered it particularly vulnerable to attack by bacteria. There is, however, no special reason to doubt that the endosperm was completely absorbed by the embryo.

Discussion

Affinities of *Enigmocarpon*

Until quite recently the affinities of the plant which bore this interesting fruit were entirely unknown. The new generic name *Enigmocarpon* was given to it in 1934 after I had failed in my attempts to obtain a clue.

Availing of a visit to London in 1935 I compared the fossil with the large collections of dried fruits at the British Museum and in the herbarium and museums at Kew, but in vain. Specimens, sections and photographs were also referred to taxonomists familiar with the modern Indian flora but without any satisfactory result. Among the genera which showed resemblances in isolated features the nearest, so far as I could see, were *Clusia* and *Garcinia* (Guttiferæ), *Apeiba* (Tiliaceæ) and *Oncoba* (Flacourtiaceæ), but none of these could be at all closely compared with the fossil. Turning to the fossil genera, we have seen that Rode's comparison (1933) with *Cucumites* Bowerbank was admittedly a very provisional one. In fact this genus had already been identified with the modern *Oncoba* by Reid and Chandler (1933, p. 408) who showed conclusively that it is neither related to *Cucumis* or any other Cucurbitaceæ nor, as Heer had believed, to *Apeiba*. With some specimens of *Oncoba* (as figured by Bowerbank under *Cucumites*) our fruit no doubt shows a striking superficial resemblance, but *Oncoba* has a parietal placentation with the seeds sunk irregularly in a pulpy, lobed placental mass. From *Apeiba* again our fossil differs, among other things, in its placentation, for in that genus the seeds are attached to the surfaces of

the septa. Finally, *Clusia* and *Garcinia* have fleshy fruits of which also the placentation is quite different.

Chaney and Mason (1934, p. 64, pl. 9, fig. 3) have figured an 8-locular fruit of *Arctostaphylos glauca* Lindl. from the Pleistocene of California; their fig. 3 generally resembles our Photo. 13, but there the resemblance ends. From the Tertiary brown coal of lower Rhineland Kirchheimer (1936, p. 116, pl. XII, figs. 12, 13) has figured under the name *Arctostaphyloides* some spherical or ellipsoid fruits of about the same size as *Enigmocarpon* ; they are 5–10 locular and have a loculicidal dehiscence. But the comparison cannot be carried further, because these are stony fruits with only one seed in each loculus.

We thus see that *Enigmocarpon* was not allied to any of the genera with which comparisons had been tried. Here the position rested until 1941, when a lucky discovery by Mr. V. B. Shukla, M.Sc., led indirectly to the clue. During a visit to Mohgaon Kalan on March 8 of that year, when we made a handsome collection of petrifactions, Mr. Shukla picked up a small silicified flower preserved in an almost perfect longitudinal fracture, of which the structure he has been investigating in detail at Lucknow, and this flower, as I soon began to suspect, belongs to the very species of plant that bore the enigmatical fruit. At the present moment the question of whether the flower and fruit belonged to the identical species is not before us. The point is that the floral characters, as Mr. Shukla found, suggested a reference to either the Primulaceæ or the Lythraceæ ; with a strong presumption in favour of the latter and this clue, when followed up in the case of the fruit (and particularly of the seed, whose anatomy I had not yet fully investigated), revealed a combination of characters leaving no room for doubt that, whatever the flower might ultimately prove to be, the *Enigmocarpon*, at any rate, belonged to no other family but the Lythraceæ.

In the hope of finding the counterpart of his unique specimen Mr. Shukla has paid repeated visits to the locality but although this hope has not been fulfilled his trouble has been amply rewarded: he has brought back numerous other specimens of the flower, which have enabled him to make a complete study of the floral organisation.

While a full exposition of Mr. Shukla's discovery is still awaited, a few of the salient facts announced by him before the December meeting of the Indian Academy of Sciences (1941) may be related here in his own words (1942, p. 221): "The preservation of most of the flowers is so perfect that it has been possible to make a complete floral diagram and floral formula. The flowers average about 6 mm. in length and are stalked. They possess a

calyx, a gamopetalous 8-lobed tubular corolla,* 8 epipetalous stamens and a shortly stalked superior 8-locular ovary with axile placentation. The anthers are seen in different stages of dehiscence; they all contain pollen-grains. A few pollen-grains have been found lying in the corolla tube. The flowers were definitely heterostylous; most of them are short-styled and the rest long-styled. The stigma is capitate."

This is, briefly, the structure of the flower. The evidence for assigning the fruit to this flower is partly circumstantial, partly structural. The circumstantial evidence is that, like the flower, the fruit is one of the commonest fossils at Mohgaon Kalan; the two are often closely associated and neither has yet been found anywhere else. In our Photo. 23 are seen two fruits collected by me in 1931 and in the same slice we find a longitudinal section of the basal part of a flower with a shortly stalked spherical ovary seated in a slightly expanded calyx tube. This being a poorly preserved partial section, the significance of this flower was not realised in 1931 but there is little doubt of its identity with the flower found by Mr. Shukla ten years later. As for the structural evidence, in so far as it is possible to compare a ripe fruit with its ovary in the flower stage, the agreement in fundamentals is clear even from the brief description just quoted, and there are resemblances in points of detail. But I must not anticipate Mr. Shukla's work, which is shortly to be published; nor, as explained, is a proof of this identity essential for ascertaining the affinities of the fruit, although admittedly it was this suspicion that really put me on the path.

To return to the fruit. The basis for referring it to the Lythraceæ may be briefly stated, it being of course understood that it is only the sum-total of the characters enumerated that constitutes the evidence : the dry capsular fruit, adapted for dispersal by water; dehiscence loculicidal, the septa coming off with the valves; the thick axile placenta; seeds numerous, anatropous, packed horizontally in vertical rows, more or less obpyramidal through mutual pressure; chalaza obliquely placed, micropyle bent towards the funicle; raphe great enlarged with spongy tissue for aquatic dispersal; funicular bundle supplying the nucellus through a hypostase; persistent nucellar epidermis and " epistase "-like apex; embryo straight, seed exalbuminous.

It would make the argument needlessly involved if I were to cite chapter and verse for each individual character, because too many of the characters are distributed over more than one family. I will therefore content myself with referring the reader in some detail to the literature that has led me to

* More probably, I think, a calyx-tube, with the stamens therefore *episepalous*, as in many Lythraceæ to-day.

the conclusion that while there is no other genus, living or extinct, which is known to combine these features, there is also no family apart from the Lythraceæ which satisfies all these conditions: Koehne [1881–1886, vol. 6, pp. 31–33; 1898, p. 5; 1903, pp. 15–17 for dehiscence and seed characters (general)]; Mauritzon (1934, esp. pp. 4, 5, 10, 13, figs. 1N, 2N, 3D for ovules of *Peplis*, *Ammannia*, *Nesaea*, *Cuphea*; 1939, p. 67, fig. 18N for expanded raphe of *Lagerstroemia*); Joshi and Venkateswarlu (1935 I, pp. 483–4, 490, figs. 1–3 for ovule of *Lawsonia*; 1935 II, pp. 523–6, figs. 1–2, 31–32 for placenta and ovule of *Lagerstroemia*; 1936 III, pp. 380, 383, 386, 396, figs. 3, 6–10, 50, 52 for placenta and ovule of *Ammannia*, *Nesaea*) ; Nikitin (1929, pp. 34–35, figs. 1–2, pl. 589, figs. 1–9 for *Decodon* spp., living and extinct, all with spongy tissue in the swollen raphe) ; Reid (1920, pp. 80–82) and Kirchheimer (1935, pp. 49–50, pl. II, figs. 8–9) for two fossil spp. of *Decodon* and for the fossil genus *Diclidocarya* with spongy tissue in lateral expansions ; Reid and Chandler (1933, pp. 415–421, pl. 21, figs. 26–31, Text-Fig. 15; pl. 22, figs. 1–7 for the extinct genera *Minsterocarpum*, with spongy tissue mainly in lateral wings, and *Pachyspermum*, raphe greatly swollen with spongy tissue).

Some other papers on the Lythraceæ, particularly those by Tischler (1917) and Souèges (1925) describing *Lythrum*, have not been accessible to me.

As Koehne warns us (1903, p. 15) the structure and mode of dehiscence of the fruit in the Lythraceæ is only of restricted value in delimiting the genera, and of course loculicidal capsules are by no means confined to this family. Some of the other features, *e.g.*, the obliquely placed chalaza and bent micropyle, are also shared by several families of the Myrtifloræ. Even such an unusual organ as the hypostase occurs not only in the related groups Melastomaceæ (Subramanyam, 1942, figs. 10, 61) and Onagraceæ (Johansen, 1928) but in several distinct circles of affinity (see Netolitzky, 1926). We find it, for instance, in the totally unrelated genus *Polygonum* (Souèges, 1919, p. 177, Fig. 24, 25) which, curiously enough, shares with *Enigmocarpon* a marked prolongation of the nucellar apex. This latter structure is again apparently of no phylogenetic significance since it occurs in such distant circles of affinity as the Polygonaceæ, Euphorbiaceæ and Cucurbitaceæ (see Schnarf, 1931, pp. 47–49, 62, 212). Similarly, the persistent nucellar epidermis is not only found in *Cuphea*, a member of the Lythraceæ, but also in the Droseraceæ, Burmanniaceæ and other families (Schnarf, 1931, pp. 95, 257, etc.), although a permanent "epistase"-like nucellar apex, recalling that in *Enigmocarpon*, seems to have been recorded elsewhere only in *Cuphea* (Mauritzon, 1934, p. 13).

Thus, while isolated features of *Enigmocarpon* are to be met with in very diverse families, even beyond the limits of the Myrtifloræ, one looks in vain outside the Lythraceæ for a family, much less a genus, combining the characters enumerated. We are therefore fully justified in regarding *Enigmocarpon* as an extinct new genus of Lythraceæ.

This affiliation finds interesting support in the fact that the fruit and seed are adapted for dispersal by water, because many Lythraceæ still frequent damp places. In fact, as we shall see, this water-loving habit was an ancient characteristic of the family, probably much more wide-spread in early Tertiary times than it is to-day. We shall revert later to this aspect of the history of the Lythraceæ ; here we need only suggest in passing that there are good grounds for regarding the spongy tissue in the seeds of many of the modern Lythraceæ, *e.g.*, *Lagerstroemia* and *Lawsonia*, which are not known for any special preference for damp habitats, as a relic of an amphibious ancestry.

With this reference of *Enigmocarpon* to the Lythraceæ the possible comparisons have been so narrowed down that it should not now be difficult to trace the nearest allies of the genus. Fortunately we possess in Koehne's monographic work, based upon many years' intensive study, as thorough and critical an analysis of the genera as one could expect on the basis of the macroscopic features. Koehne divides the family into two tribes: the Lythreæ, with the septa of the ovary incomplete above, and the Nesaeeæ, with the ovary septate from top to bottom. The Lythreæ can be at once eliminated because in our fruit the ovary is completely septate. In the Nesaeeæ there are, in Koehne's classification, two subtribes (1903, pp. 23–24):

(*a*) The Nesæineæ, with the integument neither winged nor specially thickened anywhere: *Nesæa*, *Crenea*, *Heimia*, *Decodon*, *Grislea*, *Adenaria*, *Tetrataxis* and *Ginoria*.

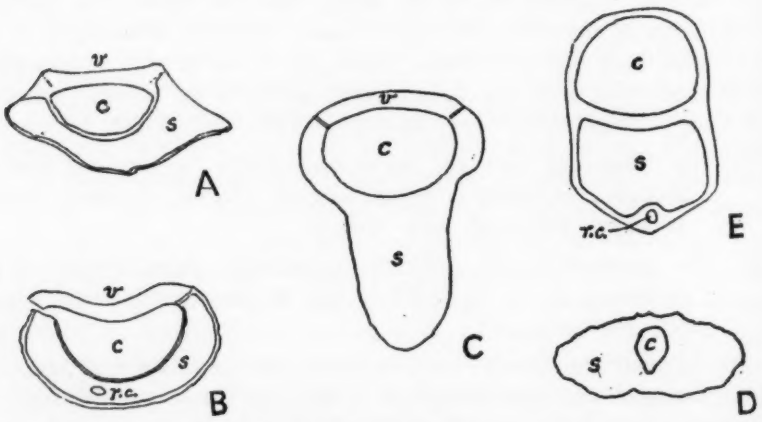
(*b*) The Lagerstroemiinæ, with the integument either winged in the median plane or markedly spongy at the apex : *Lagerstroemia* and *Lawsonia*.

The Lagerstroemiinæ are easily excluded because in the first genus the seeds are winged and the cotyledons folded, in the second the fruit is indehiscent.

Of the eight genera of Nesæineæ, *Nesæa* is out of the question because its fruit dehisces by a lid ; *Crenea* and *Adenaria* because the fruit is indehiscent ; *Tetrataxis* and *Ginoria* because of their septifragal capsules leaving the septa attached as wings on the placenta. *Grislea* has a loculicidal capsule but with only two loculi and bifid valves, while the seeds are

subglobose. The only genera admitting of a serious comparison are *Heimia* and *Decodon*, both confined at the present day to America but with *Decodon* represented by two Tertiary species in Europe (Nikitin, 1929; see Table below).

The North American species *Decodon verticillatus* approaches *Enigmocarpon* in its loculicidal capsule with obpyramidal seeds attached to a stout axile placenta; the seeds, moreover, which are about as large as in our Deccan fossil, have a raphe swollen with spongy tissue in the interior of the integument (Text-Fig. 30 A), a feature overlooked by Koehne as he did not go into the details of the seed anatomy. A median section of the seed, figured by Nikitin (*l.c.*) offers several good points of resemblance with our Text-Fig. 5, and if Nikitin's sketch were less diagrammatic other points of similarity might emerge. But in spite of all this a generic identity is ruled out by the presence in *Decodon* of a special flap of the integument on the anterior face of the seed, which serves as a germination valve—another feature not recorded by Koehne (Text-Fig. 30 A B C, *v*). This characteristic organ also occurs in both the fossil species *D. globosus* and *D. gibbosus* and accordingly must be given generic rank. (The related Tertiary genus *Diclidocarya* also has a germination valve but here it is free all round its margin, not fixed to the integument like a flap, and the spongy tissue lies in two lateral wing-like expansions. The valve is not shown in Text-Fig. 30 D.)



TEXT-FIG. 30. Cross-sections of seeds (diagrammatic). A. *Decodon verticillatus*, recent, after Nikitin. B. *Decodon globosus*, Pliocene of Russia, after Nikitin. C. *Decodon gibbosus*, Mio-Pliocene of France, after E. M. Reid. D. *Diclidocarya Menzelii*, Upper Oligocene or Miocene of Senftenberg; germination valve not shown: perhaps the section does not pass through it; after E. M. Reid. E. *Enigmocarpon Parijai*, Eocene of the Deccan; original. In all figures the ventral face is at the top. *v*, germination valve; *c*, seed-cavity; *s*, spongy tissue; *r.c.*, raphe-canal. All ×*ca.* 22.

	Eocene		? Up. Oligocene or Lower Miocene of Germany			Tertiary Brown-coal (exact age ?) of East Germany	Mio-Pliocene	Middle Pliocene		Upper Pliocene		Pleisto-cene	References
	Mohgaon Kalan (Deccan) Base of Intertrappean Series	London Clay	Niederlausitzer Brown-coal (Senftenberg)	Oberlausitzer Brown-coal	Lower Rhine Brown-coal	Gartiz a.d. Oder (Germany)	Pont-de-Gail (France)	Reuver (Holland)	Woronezh (Central Russia)	Tegelen (Holland)	Raevels (Belgium) (? Upper Pliocene)	Karewa beds of Laridura (Kashmir)	
Woodfordia fruticosa (L.) S. Kurz.												×	G. S. Puri, 1942
Decodon globosus (EMR) Nik.			×			× (?)	×	×	×	×	×		E. M. Reid, 1920, 1923, 1927 ; Nikitin, 1929 ; Kirchheimer, 1935
Decodon gibbosus (EMR) Nik.							×						E. M. Reid, 1920, 1923
Dielidocarya Menzelii .. EMR			×	×									E. M. Reid, 1927 ; Nikitin, 1929 ; Kirchheimer, 1935, 1936
Lawsonia-like seeds					×								Potonié-Gothan, 1921
Lawsonia europea (? *L. inermis*)		×											Ettingshausen, 1879 ; Potonié-Gothan, 1921
Minsterocarpum alatum R & C		×											
Pachyspermium quinquelocculare R & C		×											
Tamesicarpum polyspermum R & C		×	Provisionally referred to the Lythraceæ										Reid and Chandler, 1933
Cranmeria trilocularis R & C		×											
Enigmocarpon Parijai Sahni	×												Sahni, 1934, 1937, 1938, 1940
Silicified flowers most probably of the above species	×												Shukla, 1941, 1942

There remains for consideration only the genus *Heimia*, with two species, both belonging to the New World (Koehne, 1882, pp. 339–40; 1903, pp. 241–43). Here the loculicidal capsule has a thick axile placenta and the septa, though only 3 to 6 in number, come off with the valves as in *Enigmocarpon*; the seeds are rather small but, as in the fossil genus, their shape is cuneiform to obovate, and the epidermis of the seed-coat is papillate. So far as these characters alone are concerned there would seem to be no difference of generic rank. But while in *Enigmocarpon* the fruit wall is thick and spongy, and in a cross-section each loculus generally shows only two seeds, in *Heimia* the valves are thin and subcoriaceous, and the number of seeds is much greater. In addition, the seed of *Enigmocarpon* presents a set of well-defined anatomical features sufficient by themselves to distinguish a genus, of which, to say the least, there is no evidence at present in *Heimia*. I am unfortunately not yet in a position to compare the seed anatomy of *Heimia* but on the evidence before us it appears that while there is no known genus with which *Enigmocarpon* can be identified, its nearest living allies may have to be sought in a distant quarter of the globe : going by the seed and fruit characters the genus *Decodon* seems to me to resemble *Enigmocarpon* more nearly than does *Heimia*, but we need more data.

The seed anatomy of the different genera of Lythraceæ would probably well repay a detailed study. From the little we know of it in the living and fossil types so far examined the structure seems sufficiently rich in well-marked features to promise perhaps the most reliable basis for defining the genera.

Fossil history of the Lythraceæ

It may be useful to review briefly the growth of our knowledge of the fossil history of the Lythraceæ.

In 1879 Ettingshausen recorded from the London Clay of the Isle of Sheppey (which is well known to be of Eocene age) some fossil leaves under the new specific name *Lawsonia europæa*, but even the generic identification has never been confirmed. In 1921 Potonié and Gothan (p. 394), while referring to the London Clay species, gave the name as "*Lawsonia inermis* Ettingsh." They also mention *Lawsonia*-like seeds from the Miocene of the Lower Rhine, but of these I have seen no description. In Reid and Chandler's monograph of the London Clay Flora there is a mention (1933, p. 15) of "*Lawsonia europæa* Ett. and Gard." out of Ettingshausen's list of 1879 ; the original specimen or specimens appear to have been lost and, so far as I know, were never described or figured.

Seeds belonging definitely to Lythraceæ have been known since the year 1907 (C. and E. M. Reid) but their reference to this family—and even the fact that they were seeds—was not established until 22 years later when Nikitin (1929, pp. 33–36) cleared up their systematic position. The rather chequered history of these seeds is briefly as follows.

In 1907 Clement Reid and Mrs. Reid had figured, from the Upper Pliocene of Tegelen in Holland, certain seed-like bodies whose real nature and affinities were unknown. No name or description was given. A year later Reid (1908, pp. 589–90) described similar objects from the Pliocene of Raevels in Belgium. In 1915 these authors figured them again (this time from the Pliocene of Reuver in Holland) and published the first description of the species (Reid and Reid, 1915, p. 112, pl. 11, fig. 18). On this occasion they tentatively referred them to the modern genus *Stocksia*, suspecting them to belong to a member of the Sapindaceæ because they possessed a peculiar flap-like valve of the integument which is also found in certain members of this family and which allows the embryo to escape on germination. In 1920, however, Mrs. Reid became convinced that the reference to the Sapindaceæ was not supported by the facts; she therefore consigned them to a new genus, *Diclidocarya*, of unknown systematic position. The species was now named *D. globosa* (E. M. Reid, 1920, pp. 80–81). In the same paper a second species, found in great abundance in the Mio-Pliocene of Pont-de-Gail (Cantal, France), was described as *D. gibbosa* n. sp.; this was distinguished by the presence of a great dorsal protuberance of the integument in the region of the raphe, comparable with the condition we have described above in *Enigmocarpon*. As in this Indian genus, the protuberance contained a mass of spongy tissue presumably serving as a float for aquatic dispersal. In *D. globosa* this aerenchyma was much less developed, hence the "globose" instead of the "gibbous" form (see E. M. Reid, 1920, fig. 1, p. 81).

Both by their structure and by their association with a flora largely of aquatic plants these species of *Diclidocarya* were suspected to be aquatic forms.

In 1923 Mrs. Reid found *D. globosa* also among numerous other seeds from Pont-de-Gail, and gave a diagnosis of the species, at the same time reproducing the original description of 1907 (E. M. Reid, 1923, pp. 352–53). In 1927 she found the same species again in the Miocene (or ? Upper Oligocene) Brown-coal of Kauscha in Senftenberg (Germany), from which at the same time a third species, *D. Menzelii*, was described (E. M. Reid, 1927, pp. 3–4, pl. 580). This species differed from the other two in its

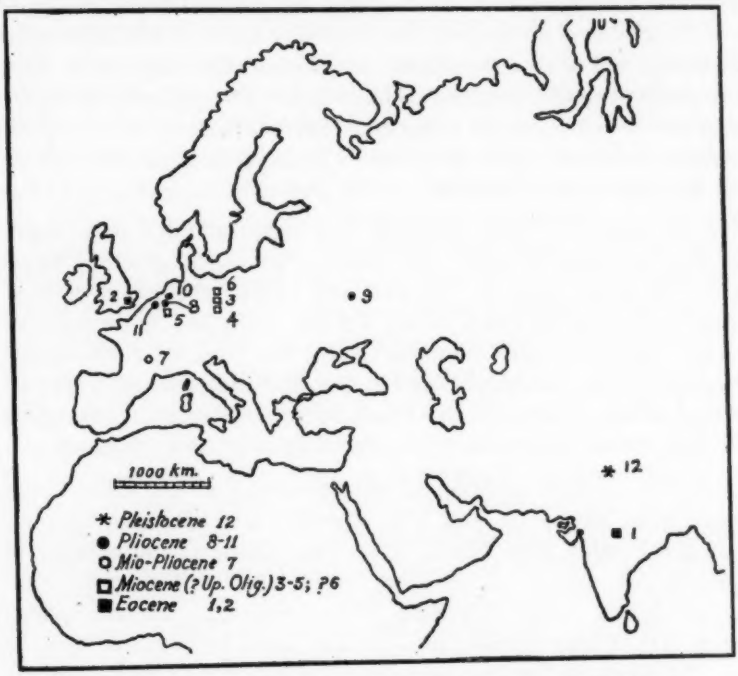
flattened form and in the smaller size and oval shape of the germination valve which, moreover, was free all round from the rest of the integument instead of being fixed to it like a flap. In this paper Mrs. Reid discusses the possibility that these " nuts " of *Diclidocarya* are true fruits, but on the whole inclines to the view that they are seeds.

Only two years later the whole problem of the nature of these bodies and their systematic position was solved by P. A. Nikitin (1929, pp. 33–36) who showed conclusively that they were the seeds of an extinct species of *Decodon*, a modern genus of Lythraceæ now confined to North America. Nikitin had discovered *Diclidocarya globosa* in certain lignitic beds of Middle Pliocene age near Voronezh in Central Russia. He writes that the strata here represent the "successive deposits of lakes, marshes and woodlands". Seeds of *D. globosa* occurred in all three zones, but he noticed that while they were found with least frequency in the lacustrine beds where aquatic plants prevailed, they were most abundant in the zone where the associated plants were woodland species. Coupling this fact with the knowledge that the seeds were structurally adapted for dispersal through water, he acutely suggested that they probably belonged to a sub-squatic, not an aquatic, plant : a conclusion which fitted in eminently with a Lythraceous affinity. Nikitin had found that in all fundamental features the fossils agreed with the seeds of *Decodon*, of which only one living species, *D. verticillatus*, is known. In fact he showed by a detailed comparison of the external features as well as of the anatomy that in *Diclidocarya globosa* we were dealing with the seed (not fruit) of an extinct but new species of *Decodon*, henceforward to be known as *Decodon globosus* (E.M.R.) Nikitin. What is more, he was able to find some indication of the size of the fruit ; for, although the walls of the fruit were not preserved, he noticed that the seeds sometimes lay grouped in their natural position in more or less spherical masses about 5·5 to 6 mm. in diameter, which agrees well with the size of the capsule in *D. verticillatus*.

We thus see that the tracking down of these elusive seeds to their true systematic position (in a monotypic genus now existing only on the other side of the Atlantic) is one of the little triumphs of palæobotanical investigation. We may add that seeds, presumably of *D. globosus*, have recently been recorded also from the brown-coal of Göritz on the Oder in East Germany, where Gothan discovered them in masses in association with numerous remains of palms (see Kirchheimer, 1935, p. 50).

Decodon globosus is thus known from 7 or 8 different localities in North-Western, Central and Eastern Europe, and ranges in geological age from the Upper Oligocene (? or Miocene) to the Upper Pliocene (see Table).

Of the remaining two species of *Diclidocarya*, *D. gibbosa* [now *Decodon gibbosus* (EMR) Nikitin] is known only from the Mio-Pliocene of Pont-de-Gail but there it occurs in great profusion. It is sharply distinguished from



Text-Fig. 31. Distribution of fossil Lythraceæ. (See Table.)

D. globosus by the great development of its dorsal protuberance which contains the spongy tissue.

As regards the third species, *Diclidocarya Menzelii*, Mrs. Reid is of the view, and I think rightly, that it is generically distinct from *Decodon*. It differs in the facts (i) that the germination valve is completely free from the integument and (ii) that while in all the three species of *Decodon* the spongy tissue extends dorsally as well as laterally to the nucellus, here it lies only (or mainly) in two lateral expansions which give the seed a dorsiventrally flattened appearance. In *Enigmocarpon*, as we have seen, this tissue lies only on the dorsal side. Thus in the position of the spongy tissue the three genera *Decodon*, *Diclidocarya* and *Enigmocarpon* are quite distinct from one another (see Text-Fig. 30).

Mrs. Reid suggests that *Diclidocarya* is closely allied to *Decodon*, but this is perhaps best left an open question till we know the seed anatomy of the several other genera in which the seed is dorsiventrally compressed (see below).

Recently Kirchheimer (1933, pl. 2, figs. 8 *a*, 8 *b*) has added to our knowledge of *Diclidocarya Menzelii* by figuring some more or less spherical seed-masses lying grouped in their original positions in the fruit cavity, although the fruit walls are not preserved. The fact that the seed masses are divided up radially into 4 to 6 sectors suggests that the fruit was a loculicidal capsule in which, as in *Decodon* and other genera, the septa came off with the valves, leaving the seed masses attached to the placenta.

Till the year 1929 *Dicl. Menzelii* had been recorded only from the Senftenberg brown-coal, which the German geologists generally regard as Miocene. Latterly, however, Kirchheimer (1936, Table opp. p. 124) has published a distribution chart of the Tertiary fruits and seeds described by him from Germany, and here he gives this species both under the Niederlausitzer Braunkohlenformation (which includes the Senftenberg brown-coal of Kauscha) and the Oberlausitzer brown-coals. He gives the age of both these formations as Upper Oligocene, not Miocene.

In 1933 a valuable addition to our knowledge of the fossil Lythraceæ was made when Mrs. Reid and Miss Chandler published their monumental work on the London Clay Flora. With their characteristic patience in the investigation of minute details they were able to distinguish four new genera of fruits, *Minsterocarpum*, *Pachyspermum*, *Tamesicarpum* and *Cranmeria* (1933, pp. 415–25, pls. 21, 22), each represented by a single species. Of these the first two were definitely assigned to the Lythraceæ, the last two provisionally.

Minsterocarpum alatum had a usually 4-locular subcylindrical loculicidal capsule with the seeds attached horizontally to a thick axile placenta in two longitudinal rows in each loculus. The seeds were compressed in a plane which the authors cautiously do not define as lateral although a cross-section figured by them (Text-fig. 15, p. 417) might tempt one to regard it as such. The two wing-like expansions at the sides of the seed body were thick and composed of a spongy tissue which also covered one face of the seed so as to form a bridge over it connecting the two "wings", the other face showing a depression over the seed body. The seed was thus embraced by the spongy tissue on three sides. The authors regard this genus as a near ally of the modern *Lagerstroemia*, but in this genus the wing is said to be formed by the expansion of the raphe in the median plane, and the distribution of spongy tissue is very different.

In *Pachyspermum* the fruit is described as a "five-loculed, almost certainly septicidal, capsule having anatropous seeds with swollen raphes attached to prominent axile placentas". The raphe was spongy and, as in *Enigmocarpon*, much larger than the seed body, which it partially embraced. The affinities of the genus within the Lythraceæ are obscure.

The next contribution to the fossil record of the Lythraceæ was Mr. V. B. Shukla's important discovery, at Mohgaon Kalan, of the exquisitely preserved flowers already referred to above, of which a full account will be awaited with interest (Shukla, 1941; 1942, p. 221). As suggested above, these flowers almost certainly belonged to the same plant that bore the fruit known for the last nine years as *Enigmocarpon Parijai* but now for the first time described in full. From what has passed above it will be agreed that these Deccan fossils (flowers and fruits) represent by far the best preserved and most completely known extinct member of the family, besides being, in all probability, the oldest in the geological sense.

Judging from their history in the Tertiary period and their geographical distribution to-day, the Lythraceæ must certainly have been fairly widespread during the Pleistocene ; but I have not come across any mention of them in the literature so far as I have able to consult it. However, Mr. G. S. Puri, M.Sc., who is preparing at Lucknow a comprehensive memoir on the Pleistocene flora of Kashmir, tells me that he has collected a leaf, identified by him with the modern *Woodfordia fruticosa* (L.) S. Kurz* from the Karewa beds at Laridura (alt. *ca.* 6,000 ft.) near Baramulla. This species exists commonly to-day in the Deccan and extends into the outer ranges of the Himalayas up to an altitude of about 5,000 ft.

The accompanying Table gives a summary of the known fossil record of the Lythraceæ. From a critical review of their present distribution Koehne (1886, p. 32) had assigned to them an age not exceeding that of the mammals. We see that palæobotanical research since then has not revealed any trace of their existence before the dawn of the Tertiary era, but even the early Tertiary Lythraceæ are so highly evolved that the existence of this family in Cretaceous times would not appear at all unlikely. As our fossil data increase it would be interesting also to examine Koehne's deductions about the relative antiquity and migrations of the different genera, now scattered over all but the highest latitudes of the globe. At the same time, as suggested, a comparative study of the seed anatomy should help towards a better understanding of the interrelations of the genera, living and extinct, and afford useful clues to the means of dispersal that lay open to

* More commonly, but I think incorrectly, known by the name *W. floribunda* Salisb.

them during the 60 or 70 million years of their history since the dawn of the Tertiary era.

No one who has even cursorily examined the seeds of the known fossil Lythraceæ can fail to be impressed by the part which water must have played in their dispersal. All the known species of *Decodon*, living and extinct, as well as the Eocene genus *Pachyspermum*, possess a raphe markedly swollen with spongy tissue, undoubtedly a floating mechanism like that in the seed of *Enigmocarpon* ; and in this genus the entire fruit, down to the septa and the placental column, is spongy. In the genera *Diclidocarya* and *Minsterocarpum* the seed is compressed and most of the spongy tissue lies in thick wing-like expansions. *Lawsonia* has a thick spongy mass at the apex of the seed. Thus nearly all the species known in the fossil state were adapted for dispersal by water. The data are still meager but so far as they go they indicate that the family was from its origin adapted to an amphibious existence and that during the course of evolution some of the genera have spread into drier situations. The thick spongy expansions of *Diclidocarya* and *Minsterocarpum* may have served for wings as much as for floats. In *Lagerstroemia*, where the distal part of the raphe is compressed in the median plane, the wing still retains its spongy character near the seed body where it is thickest. Koehne (1903, p. 16) mentions several modern genera with their seeds flattened in the dorsiventral plane (*Cuphea*, *Ginoria*, *Diplusodon*, *Pemphis*, *Lafoënsia*), the expansion in some being thick and spongy, in others thin and membranous. There seems nothing strained in the idea that some of these membranous wings have been derived by flattening from the spongy floats of amphibious ancestors : in *Lagerstroemia* we see the float actually passing into the flat wing.

Associated with *Enigmocarpon* have been found the remains of many other plants indicating an aquatic or amphibious mode of life ; some of these have been briefly noticed in the literature cited. There is no need to reiterate the evidence this flora provides for an early Tertiary age for the Intertrappean beds and therefore for the Deccan Traps in this part of the Central Provinces (Sahni and Rode, 1937, p. 169). The occurrence of an undoubted member of the Lythraceæ only strengthens this evidence because no trace of this family has yet been found in any older rocks.

After Rode's discovery of *Nipa* in this locality, I suggested in 1934 (p. 136) that Mohgaon Kalan lies near the mouth of an extinct river which probably flowed into a southern arm of the Tethys Sea in early Tertiary times. The fruit and seed of *Enigmocarpon* show an unusually thorough adaptation for transport by water : they both had a durable construction, such as

might easily withstand long immersion, even in salt water. These features accord well with the fact that, so far as we know at present, the nearest allies of this Deccan plant are to be found in the New World. The modern genus *Heimia* and the related *Decodon* may have differentiated from some early Tertiary forms related to *Enigmocarpon* which migrated by way of the Tethys Sea. The occurrence of at least two good genera of Lythraceæ in the Eocene of England, both well fitted for dispersal by water, may be a further indication of the facilities for ocean travel which the early members of this family shared with so many tropical forms in the London Clay Flora (see Reid and Chandler, 1933, p. 61).

Summary

Enigmocarpon Parijai is one of the commonest of the silicified fruits in the chert beds at the base of the Intertrappean Series at Mohgaon Kalan in the Deccan. The structure shows a combination of characters found in no other known genus and only in the family Lythraceæ; its nearest known allies are the genera *Decodon* and *Heimia*.

Both fruit and seed were adapted for aquatic dispersal and seem to have been fitted for long immersion in brackish water. Among associated fossils are the remains of many other aquatic or marsh plants, including a species of *Nipa*, an estuarine genus known for its wide distribution along the coast of the old Tethys Sea, nearly always in strata of Eocene age.

The occurrence of *Enigmocarpon* in this flora lends further support to a Tertiary age for the Deccan beds, because no trace of Lythraceæ has yet been found in any older rocks.

The author gives a sketch of the geological history of the Lythraceæ. Fossil representatives of the family are now known from the Eocene of the Thames basin and of the Deccan; from rocks of Oligocene to Miocene age in several parts of Germany; from the Mio-Pliocene of France ; from the Pliocene of Holland, Belgium and Central Russia; lastly, from the Pleistocene (Karewa beds) of Kashmir.

There is good evidence that the amphibious habit still seen in many Lythraceæ was an ancient characteristic of the family, much more wide-spread in early Tertiary times than it is to-day. The spongy tissue in the seeds of some modern genera, *e.g.*, *Lagerstroemia* and *Lawsonia*, which are not known for any special preference for damp habits, is probably a relic of an amphibious ancestry.

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EXPLANATION OF PLATES

The photographs are all from untouched negatives. The figured specimens and sections are in the author's collection.

PLATE II

Enigmocarpon Parijai

Fig. 1. Two fruits fractured in different planes, exposed on a freshly broken surface of chert (see Photos. 22, 23). Nat. size.

Figs. 2–3. Two fruits exposed on the weathered surface of chert. Nat. size.

Fig. 4. Impressions of several fruits showing rows of pits left by the distal ends of the rows of seeds. In the bottom specimen the impression of the thick fruit wall is also preserved (on the left). Nat. size.

Fig. 5. A fruit cut at about 45° to the axis, showing the hollow placental column and 8 radial septa between which lie the loculicidal sutures in the thick spongy fruit wall. The positions of the septa are marked by dashes in Fig. 6. ×*ca.* 6½.

Fig. 6. The same section (central portion) after further grinding, to show details of the anatropous seeds cut in different planes. The dashes round the margin of the photograph indicate the positions of the 8 septa. Several of the seeds are shown further enlarged in Text-Figs. 12, 13. For * see Photo. 11 and Text-Figs. 28, 29; for × see Photo. 12; for ⊙ see Text-Fig. 27. ×15.

PLATE III

Enigmocarpon Parijai

Fig. 7. A fruit cut in an obliquely longitudinal plane, with a slender stalk bent to one side. The base is slightly invaginated. Nat. size.

Fig. 8. The same. ×*ca.* 2.

Fig. 9. A dehisced fruit seen from the apical end, showing 5 of the valves. ×2.

Fig. 10. The same fruit seen longitudinally fractured, with the seeds placed in vertical rows upon the thick axile placenta. ×2.

Fig. 11. Oblique surface section of the seed at * in Fig. 6, showing (*e*) epidermis of integument, composed of more or less polygonal slightly sinuous-walled cells, each with a central hyaline papilla; (*f*) the subepidermal zone of fibres; and (*s*) the internal mass of rounded thin-walled cells (spongy tissue) which forms the greater part of the raphe. Compare with Photo. 12 and Text-Fig. 28. ×180.

Fig. 12. Section cut in a plane vertical to the surface of the seed at × in Fig. 6, showing the same zones as in Photo. 11. The fibres here lie in two distinct layers, in which they run in different directions. *e*, epidermis; *ff*, fibres; *s*, spongy tissue. ×350.

Fig. 13. An undehisced fruit with 9 carpels, seen from the basal end. ×2.

Fig. 14. Opaque slice of a fruit cut tangentially through three loculi. The middle loculus shows the two rows of seeds placed back to back, mostly cut in transverse planes at different levels, between the chalaza and micropyle (*cf.* Text-figs. 9, 11). To the bottom left is a portion of a second fruit. ×2.

Figs. 15–16. The same slice, ground into a thin section. The pencilled label in Fig. 15 was written on the ground surface of the glass slide and then sealed up in a drop of Canada-balsam under the coverglass. Fig. 15 nat. size, Fig. 16 ×4.

PLATE IV

Enigmocarpon Parijai

Figs. 17–18. A denisced fruit cut transversely, showing the hollow axile placenta, and the 8 valves of the fruit wall, each with a septum attached to its middle. All the septa and seeds have broken away from the placenta. In each loculus a double row of seeds placed more or less horizontally. During fossilisation the fruit has shrunk away from its original cavity in the matrix (which is a volcanic ash), while the intervening space and all the chinks in the interior of the fruit have been filled up with transparent silica. One of the seeds (bottom left) is drawn in Text-Fig. 23. Fig. 17 nat. size; Fig. 18 ×*ca.* 4½.

Fig. 19. One of the seeds from Photo. 23. In the seed-cavity lies the obliquely cut persistent nucellar membrane. The epidermis of the integument, seen in tangential section, shows numerous hyaline papillæ (*p*); (*s*) spongy tissue of raphe; (*i*) may be an appressed inner integument, *but see text.* ×70.

Fig. 20. The nucellar membrane in oblique tangential section, near the chalazal end of the seed drawn in Text-Fig. 23. ×180.

Fig. 21. Part of the spongy fruit wall. The external surface is to the *right.* ×*ca.* 25.

PLATE V

Enigmocarpon Parijai

Fig. 22 (inset in Fig. 23). Two fruits (the same as in Photo. 1), both cut in an obliquely tangential plane, which passes through four of the loculi. Nat. size.

Fig. 23. The same fruits, enlarged. The seeds in each loculus are closely packed in two alternating rows and flattened into angular (prismatic) forms. Some of these are shown diagrammatically in Text-Figs. 6, 7, 8, 10. (*k*)? persistent calyx. In the top right corner of the photograph there is a tangential longitudinal section of the basal part of a flower, with a short-stalked ovary seated in a perigynous calyx tube; this is almost certainly a flower of the same species as the fruit (see Shukla, 1941, 1942). In the top centre, sections of some charred leaves (structure not well preserved). Near the bottom margin some free-lying seeds, one of them definitely of the same species. The matrix is a volcanic ash deposited on water. ×*ca.* 5.

Fig. 24. Another fruit (the same as that shown in Photo. 25). Some of the seeds are still attached to the axile placenta to which a few of the septa are also seen attached. The spongy fruit wall already shows the 8-loculicidal sutures. One of the two seeds at the top right shows the curved micropyle cut longitudinally. The dark colour of the seeds is mostly due to the spongy tissue; the oval spaces represent the cavity of the seed-body. ×10.

PLATE VI

Enigmocarpon Parijai

Fig. 25. A dehisced fruit in cross-section (see Photo. 24). The thick-walled outermost layers of the carpels form a well-defined dark zone. In the matrix of tuff are embedded some fragments of charred leaves in vertical section (structure poorly preserved). ×2.

Fig. 26. Slightly oblique cross-section of the axile placenta, showing (1) the remains of a delicate central tissue surrounded by (2) a vascular ring; (3) the compact inner cortex and (4) lacunar outer cortex. From a peel section made by Dr. A. R. Rao. See also Text-Fig. 3 and compare Text-Fig. 2. ×25.

Fig. 27. Two of the seeds from the left-hand fruit in Fig. 23, showing the enormous development of spongy tissue in the raphe. In the seed-cavity the embryos have been cut across the region of the radicle. The membrane round the embryo is the persisting nucellar epidermis or ? cuticle (*cf.* Fig. 19). A vascular bundle runs along the mid-dorsal line of the raphe, enclosed in a fibrous sheath (the outer part of the sheath is here damaged). Along the top of the figure a septum shows its spongy texture, somewhat like that of the outer fruit wall. Towards the bottom left of the figure are portions of two neighbouring seeds in the same loculus. ×*ca.* 42.

Fig. 28. One of the seeds from the left-hand fruit in Fig. 23 (see also Text-Fig. 10). Owing to the oblique plane of section the lateral width of the raphe is greatly exaggerated. Raphe canal on dorsal side; two slightly concave cotyledons in the seed-cavity, with traces of the nucellar membrane lining the integument. The papillæ of the epidermis of the integument are seen as a row of white dots, specially on the left; *cf.* Fig. 19. ×*ca.* 42.

Fig. 29. A seed cut in oblique longitudinal section near the median plane. *e*, epidermis of integument; *f*, fibrous layer; *n*, nucellus; *s*, spongy tissue of raphe; *i*, integument; *st*, funicle. The nucellar cap persists as an "epistase"; its tip is drawn out into a long bristle-like process. Compare Text-Fig. 21. ×*ca.* 45.

Fig. 30. Another seed similarly cut. On the left the base of the nucellus has shrunk away from the hypostase (*h*) on which it was seated; the epistase is drawn out into a process as in Photo. 29. Compare Text-Fig. 22. The cross marks the spongy tissue in the raphe of an adjoining seed. ×*ca.* 45.

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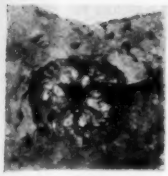

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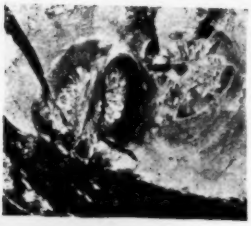

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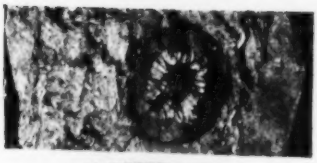

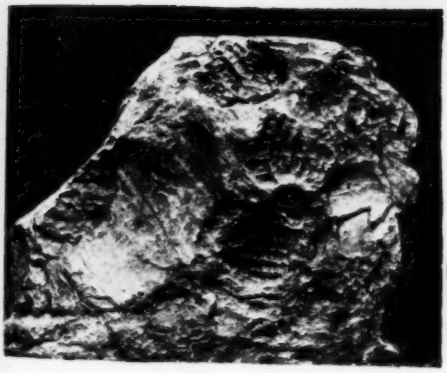

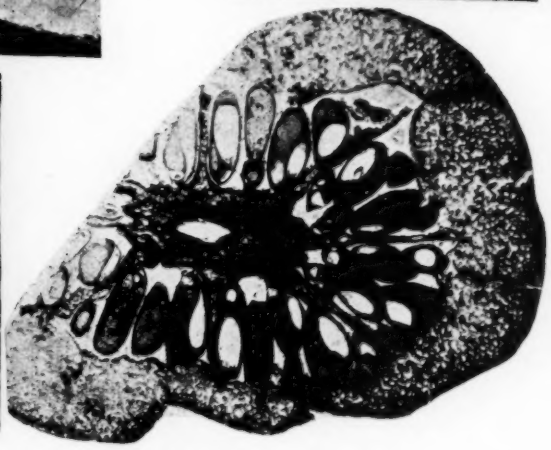

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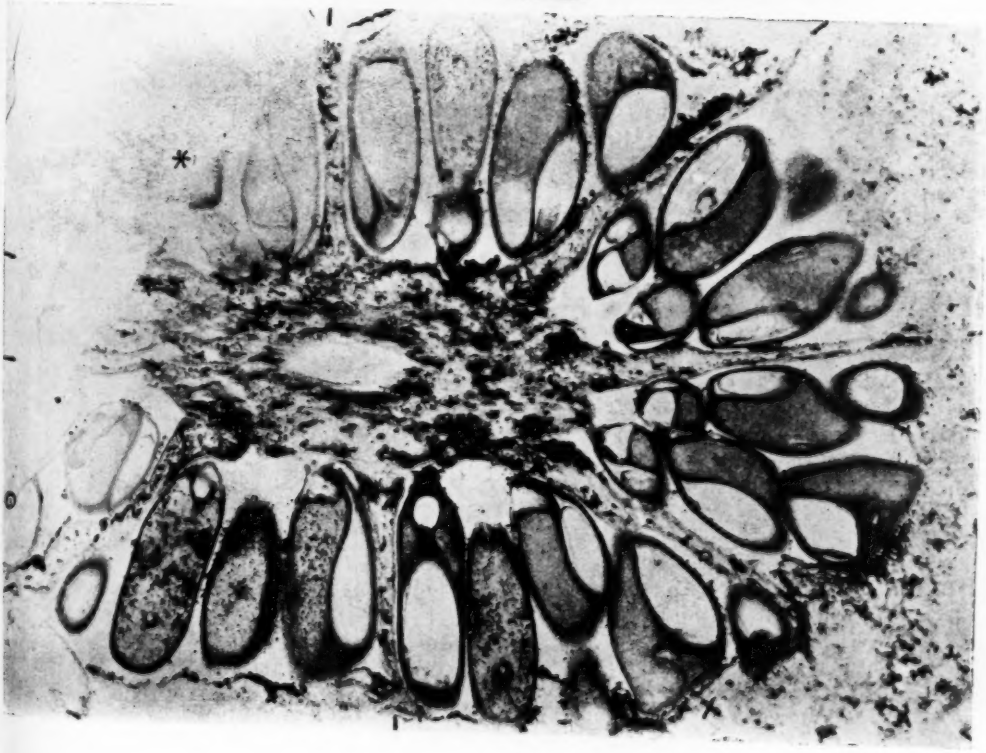

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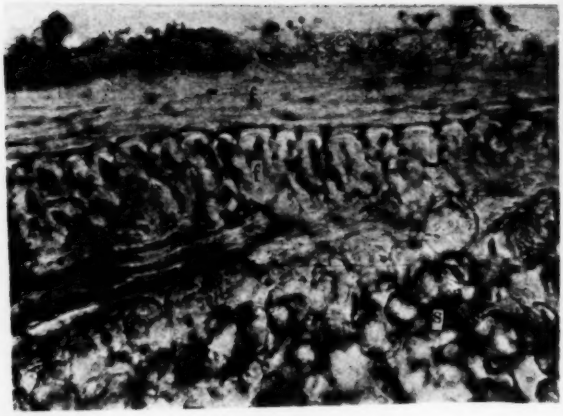

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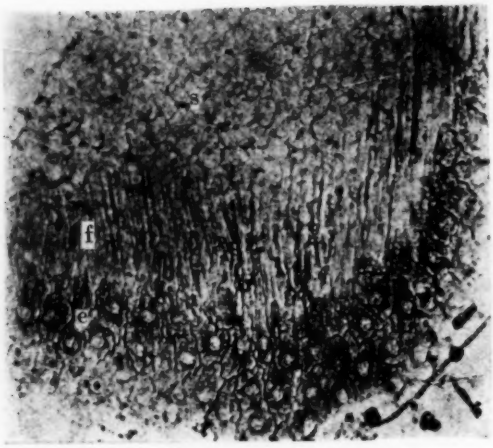

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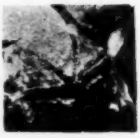

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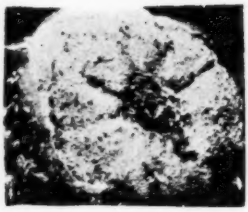

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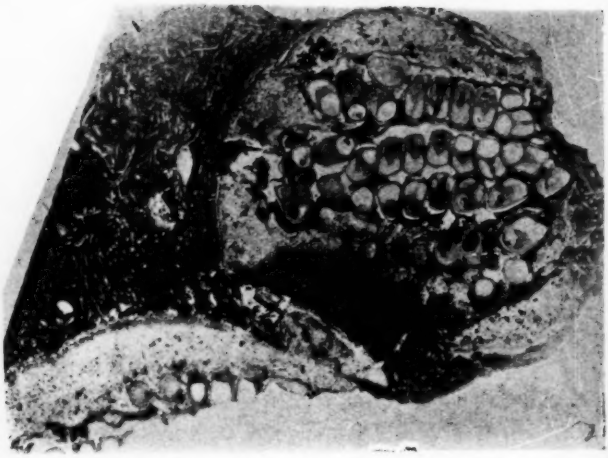

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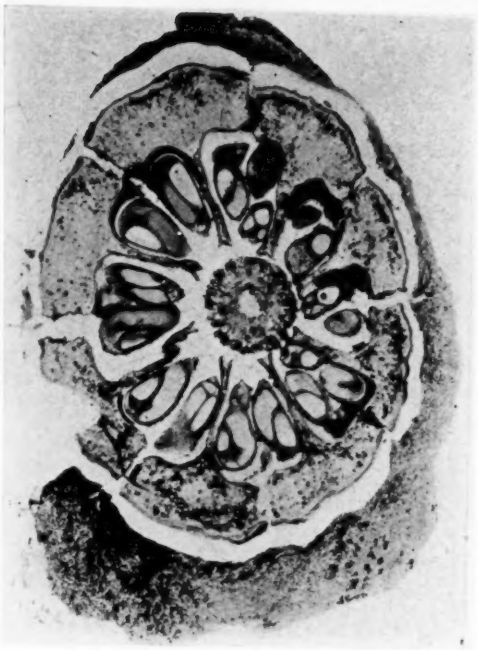

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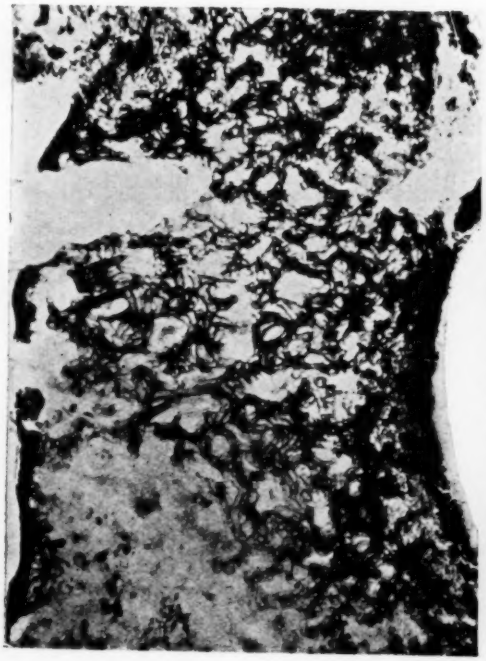

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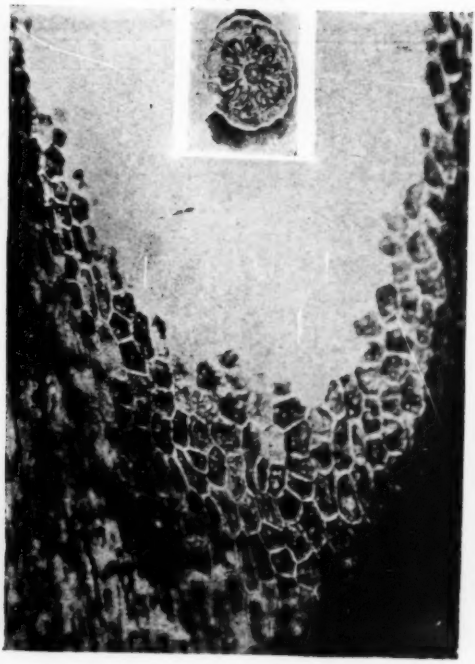

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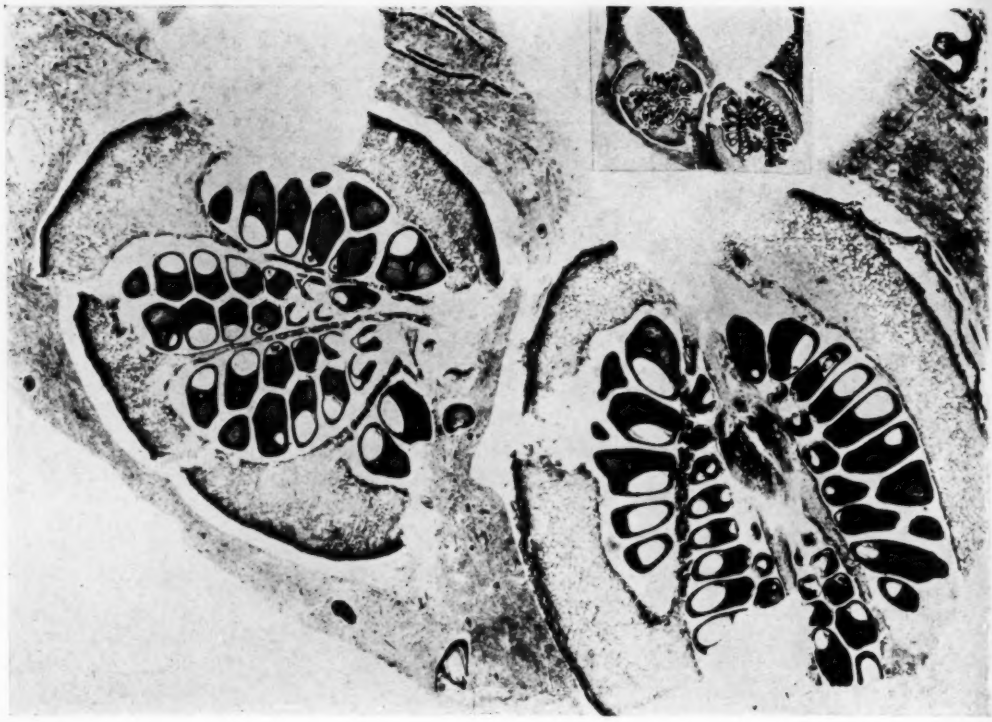

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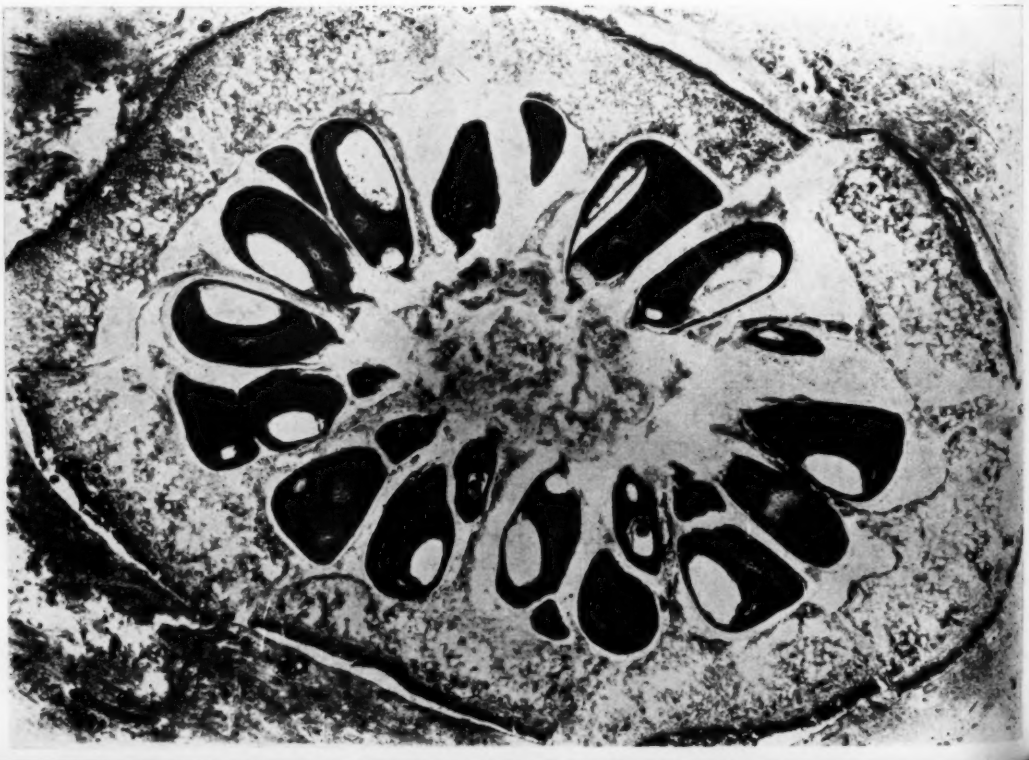

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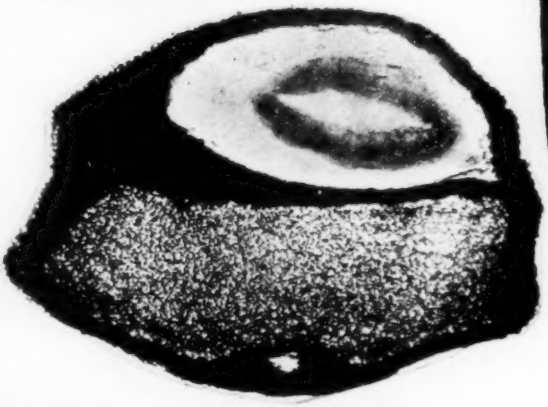

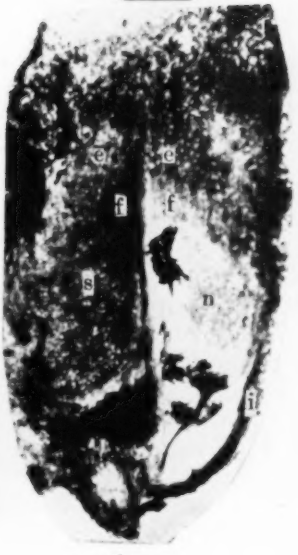

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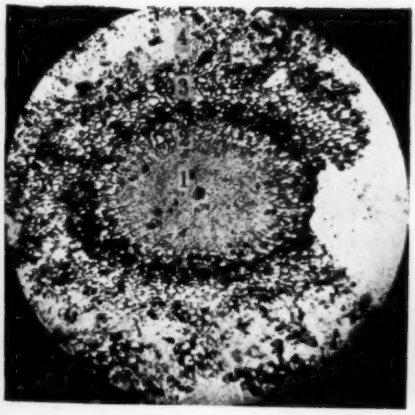

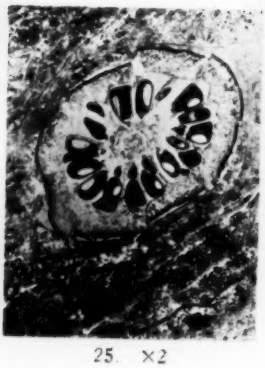

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TREMATODES FROM INDIAN MARINE FISHES

Part II. On Some Trematodes of the Gasterostome Family *Bucephalidæ* (Braun, 1883) Poche, 1907, with Description of Four New Species

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CLASS.. .. *Trematoda* Rud., 1808
ORDER .. *Digena van* Beneden, 1858.
SUB-ORDER .. *Gasterostomata* Odhner, 1905.
FAMILY .. *Bucephalidæ* Poche, 1907.
(Syn.: *Gasterostomidæ* Braun, 1883.)

EXCELLENT accounts of the history of the sub-order *Gasterostomata* and the family *Bucephalidæ* Poche, 1907 (Syn.: *Gasterostomidæ* Braun, 1883) and of the two sub-families *Bucephalinæ* Nicoll, 1914 and *Prosorhynchinæ* Nicoll, 1914, are given by Eckmann (1932), Bhalerao (1937), Nagaty (1937) and Manter (1940).

The family was originally created by Braun in 1883 under the family name *Gasterostomidæ*, for the genus *Gasterostomum* Siebold, 1848. In the same year Ziegler observed that the genus *Gasterostomum* Siebold, 1848, is synonymous with the genus *Bucephalus* Baer, 1827. In 1907, Poche

named the family *Bucephalidæ*. Fuhrmann (1932) regards *Gasterostomidæ* Braun, 1883 as the valid family with *Bucephalidæ* Poche, 1907, as a synonym to it. However the later authors refer it under the latter name only.

SUB-FAMILY .. 1. *Bucephalinæ* Nicoll, 1914.
GENUS .. 1. *Bucephalopsis* (Diesing, 1855) Nicoll, 1914.
(Syn.: *Prosorhynchoides* Dollfus, 1927.)

Bucephalopsis microcirrus. n. sp.

[TEXT-FIGS. 1, 1 (*a*)]

Four specimens of this gasterostome were found in the alimentary canals of two out of nearly eight specimens of a marine fish, *Sciæna belengeri* examined in the month of December 1940. All the forms except one were sexually mature. On examination it is found that they represent a new species of the genus *Bucephalopsis*.

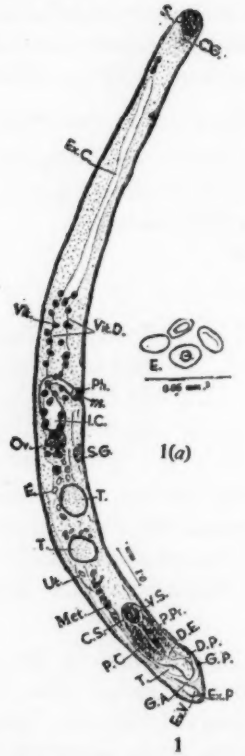

FIG. 1. *Bucephalopsis microcirrus*, n.sp FIG. 1 (*a*). Eggs (magnified)

C.G., Cytogenous glands; *C.S.*, Cirrus sac.; *D.E.*, Ductus ejaculatorius; *D.P.*, Dorsal process (genital lobes); *E.*, Egg; *Exc.*, Excretory canal; *Exc. P.*, Excretory pore; *Ex. V.*, Excretary vesicle; *G.A.*, Genital atrium; *G.T.*, Genital tongue; *G.P.*, Genital pore; H., Hoop or Cephalic disc; *I.C.*, Intestinal canal; *m.*, Mouth; *Met.*, Metraterm; *Ov.*, Ovary; *Ph.*, Pharynx; *P.C.*, Prostrate gland cells; *P.Pr.*, Pars prostatica; *S.*, Sucker; *S.G.*, Shell gland *T.*, Testis; *Ut.*, Uterus; *Vit.*, Vitellaria; *Vit.D.*, Vitelline duct; *V.S.*, Vesicula seminalis.

Body very much elongate and in natural position crescent-shaped, with a flat and slightly tapering anterior end. The posterior half of the animal contains almost all the important organs. The posterior extremity is broadly rounded. Body of the living parasite is covered over by minute spines which are more closely set in the anterior region than in the posterior. Living specimens are usually covered with mucus and they present an absolutely white, transparent appearance with dark brown dots representing vitelline follicles and golden yellow specks representing eggs. Body length is 1·71 mm., width 0·12 mm. (about 1/8 body length), maximum width being in the region of the testes. Anterior sucker (*S.*) is oval and subterminal and is situated slightly obliquely. It measures 0·016 × 0·04 mm., and, as is usual in this genus, is surrounded by unicellular glands. The deeply staining mass of glandular material (*C.G.*), just posterior to the sucker on the mid-ventral side, is dense and voluminous. It probably represents the "Cytogenous organ" of Tennent (1906) and the "penetration organ" of Woodhead (1929). Chandler (1935) observed that in the case of *Rhipidocotyle transversale* Chandler, 1935, the anterior sucker develops in the midst of this mass and vitelline follicles from its posterior part. Previous authors have recorded the presence of this material only from very young specimens but I observed it in some completely adult forms with mature eggs though its volume decreases with the advance in age of individuals. Mouth (*m.*) is a simple inconspicuous opening situated ventrally at a distance of 0·9 mm. from the anterior end. It is surrounded by a small, compact, muscular and globular pharynx (*Ph.*) which measures 0·022 × 0·03 mm. Oesophagus is a narrow, thin, straight tube running across the width of the animal, measuring about 0·075 mm. in length, posteriorly it bends to lead into the very thin-walled, ovoid intestine. The intestine (*I.C.*) runs in the antero-posterior direction, and is about 0·1 mm. in length and 0·055 mm. in maximum width which is in its posterior region.

Testes (*T.*) two, globular, post-ovarian, median, tandem, and separate. The anterior testis is slightly larger than the posterior one. It measures 0·075 × 0·06 mm. and is situated at a distance of 0·08 mm. from the ovary. The posterior one is smaller, measuring 0·065 × 0·064 mm. and is situated at a distance of 0·095 mm. from the anterior one. Cirrus sac (*C.S.*)

is a median, ovoid, highly developed muscular organ, measuring 0·22 mm. (about 1/8 to 1/9 body length). Anteriorly it comes to within a distance of 0·12 mm. from the posterior testes; posteriorly it extends almost to the end. It encloses at its anterior end a compact, ovoid vesicula seminalis (*V.S.*), 0·045 mm. in length; a well-developed elongate pars prostatica (*P.Pr.*) surrounded by prostrate gland cells (*P.C.*) and a narrow ductus ejaculatorius (*D.E.*). The genital tongue (*G.T.*) extends into the large globular genital atrium (= genital sinus) (*G.A.*) which opens medianally to the outside on the ventral surface, a little in front of the hind end, through an inconspicuous genital pore (*G.P.*). There are developed two processes (*D.E.*) dorsal to the genital tongue. The left dorsal genital lobe (= genital papilla) is fingerlike, double structure, smaller than the right. The right lobe is longer, thicker and tongue-shaped.

Ovary (*Ov.*) globular with a small protuberance on the right side, partly lying over the posterior end of the intestine. It measures 0·05 × 0·04 mm. Vitelline glands (*Vit.*) are composed of a few, large and round follicles, their average measurement varying from 0·013 to 0·02 mm. The follicles are arranged in two lateral, longitudinal, widely separated groups of 15 and 17 on the right and left sides respectively. They extend from half the distance between the ovary and anterior testis to a region much anterior to mouth. The average length of vitellarian extent on either side is about 0·38 mm. The two vitelline ducts (*Vit.D.*) are clearly noticed. The shell gland (*S.G.*) is situated to the extreme left border of the body, slightly posterior to the ovary. It is a compact pear-shaped body measuring 0·045 × 0·025 mm. The uterus (*Ut.*) does not consist of heavy coils and is longitudinal in extension. It runs by the right side of the anterior testis, takes a turn to the left of the posterior testis and finally runs on the right side of the cirrus sac as a thick metraterm (*Met.*) and opens into the genital atrium.

The excretory system consists of a tube (*Ex.C.*), extending much farther forward in the anterior region upto about 1·7 mm. from the anterior end. Posteriorly it dilates into a pear-shaped vesicle (*Ex.V.*) in the region below genital atrium and opens terminally by means of an excretory pore (*Ex.P.*).

Eggs (*E.*) are few, thin-shelled and oval. They measure 0·0035 × 0·0023 mm. (average).

The species described above possesses a simple sucker and thus belongs to the sub-family *Buceophalinæ* Nicoll, 1914. The genera included in this sub-family are *Dolichoenteron* Ozaki, 1924, in which the ovary lies between the two testes ; *Bucephalus* Baer, 1827, in which sucker bears tentacles;

Rhipidocotyle Diesing, 1858, in which the weak sucker bears a hood and *Bucephalopsis* (Diesing, 1855) Nicoll, 1914, in which the anterior end is provided with nothing but a sucker. The species described here belongs to the genus *Bucephalopsis* (Diesing, 1885) Nicoll, 1914.

The genus was originally created by Diesing (1855) as one of the two sub-genera of the genus *Bucephalus* Baer, 1827. Subsequently Nicoll (1914) raised it to the generic rank.

Eckmann (1932) published an excellent review of the group. She regarded only eight species of the genus as valid, *viz.*, *B. gracilescens* (Rud., 1819) ; *B. haimeanus* (Lacaze-Duthiers, 1854) ; *B. triglæ* (van Beneden, 1870) ; *B. arcuata* (Linton, 1900) ; *B. pusilla* (Stafford, 1905) ; *B. exilis* Nicoll, 1915 ; *B. lata* Ozaki, 1928 and *B. elongata* Ozaki, 1928.

Subsequent to Eckmann's work, Verma (1936) described five new species of the genus, *viz.*, *B. fusiformis* ; *B. garuai* ; *B. magnum* ; *B. confusus* and *B. minimus*. Of these the last three are in the opinion of Bhalerao (1937), synonymous with *B. garuai*.

Bhalerao (1937) described a new species *B. karvei* and gave a key to the species of the genus which was an enlargement of one published by Eckmann in 1932.

Since then, following more species have been added to the genus *B. scrombropsis* Yamaguti, 1938; *B. belonea* Srivastava, 1939; *B. southwelli* Nagaty, 1937 ; *B. longicirrus* Nagaty, 1937 ; *B. megacetabulus* Nagaty, 1937 and *B. longoviferus* Manter, 1940.

Unfortunately I could not get Yamaguti's paper in spite of my best efforts.

Srivastava (1939) is inclined to accept *B. magnum* Verma, 1936, as a valid species but maintains that *B. confusus* Verma, 1936, and *B. minimum* Verma, 1936, are synonymous with *B. garuai* Verma, 1936. Nagaty (1937) rightly regards *B. confusus* Verma, 1936 and *B. minimus* Verma, 1936 as synonymous to *B. magnum* Verma, 1936, and not to *B. garuai* Verma, 1936, as held both by Bhalerao and Srivastava. I have included *B. magnum* in the key.

B. tergestinum (Stossich, 1883) ; *B. ovatus* (Linton, 1900) ; and *B. Ozakii* (Ozaki, 1928) Nagaty, 1937, have been added to the list of valid species.

B. belonea Srivastava, 1939, shows close resemblance to *B. southwelli* Nagaty, 1937. They are also obtained from the same host.

Stafford (1904) described a species, *Gasterostomum pusillum* without any figure. From Stafford's description one cannot distinguish between his

species and *B. arcuata* (Linton, 1900). Eckmann (1932) could also not separate the two in her key. Nagaty (1937) therefore considered *B. pusilla* (Stafford, 1904) as a synonym to *B. arcuata* (Linton, 1900). Manter (1940) states that more recent figures of *B. pusilla* (Stafford, 1904) by van Cleave and Mueller (1934) together with Woodhead's (1930) description show that *B. pusilla* is smaller, with larger eggs and its excretory vesicle extends much farther forward. On this authority, I have included *B. pusilla* as a valid species in my key.

The new species described in this paper differs from all the known species of the genus in its very elongated shape, having a width equal to $\frac{1}{8}$ body length and in the anterior extension of the excretory vessel, which extends almost to the anterior end. Though it is a very long form its cirrus sac is comparatively very small. The extension of vitellaria anterior to intestine and pharynx, the position of the ovary at the posterior end of elongated intestine, the clear space between the ovary and anterior testis and between the two testes, a short and oval cirrus sac are characteristics which separate it from all the known forms.

HOST .. *Sciæna belengeri.*
LOCATION .. Alimentary canal.
LOCALITY .. West Coast of India, Bombay.

There are now 22 valid species in this genus and with a view to facilitate their identification a key is given below :—

A Key to the Species of the Genus Bucephalopsis (Diesing, 1855) Nicoll, 1914

1. Excretory bladder Y-shaped 2
   Excretory bladder tubular 3
2. Vitelline follicles bilobed, large, uterine coils extend on both sides of the body upto near the anterior extremity, ovary anterior to pharynx....*B. garuai* Verma, 1936.
   Vitelline follicles round, small, uterine coils lie mostly in the posterior half of the body and principally on the left side, ovary near equatorial line....*B. magnum* Verma, 1936.
3. Vitelline glands compact 4
   Vitelline glands extending like a band along the sides of the body 11

4. Testes lying on opposite sides of the pharynx..*B. haimeanus* (Lacaze-Duthiers, 1854)

   Testes lying on the same side of pharynx.. 5

5. Cirrus sac half or more than half the body length 6

   Cirrus sac less than half the body length 7

6. Pharynx at or about the posterior third, ovary in the anterior third, anterior to pharynx, vitellaria in the anterior region....*B. karvei* (Bhalerao, 1937).

   Pharynx in the anterior third, ovary at about the middle, posterior to pharynx, vitellaria slightly above the middle of the body....*B. longicirrus* (Nagaty, 1937).

7. Vitellaria slightly above the middle of body, ovary in the region of vitellaria. Pharynx at about the middle of body....*B. tergestinum* (Stossich, 1883).

   Vitellaria confined nearly to the anterior extremity, ovary situated posterior to vitellaria. Pharynx in or about the posterior half 8

8. Ovary situated in the posterior half of body along with testes....*B. Ozakii* (Ozaki, 1928) Nagaty, 1937.

   Ovary situated in the anterior half or about the middle of body 9

9. Anterior testis situated behind the intestinal sac, ovary in between vitellaria and intestine....*B. fusiformis* Verma, 1936.

   Anterior testis situated at the level of intestinal sac, ovary in or about the region of intestine 10

10. Large form, vitellarian follicles big, eggs small and many, anterior sucker very big....*B. megacetabulus* Nagaty, 1937.

    Smaller form, vitellarian follicles small, eggs bigger and few, anterior sucker smaller....*B. lenti* Nagaty, 1937.

11. Body more or less round, ovary lying near the right side of the body and far removed from testes .. *B. lata* Ozaki, 1928.

    Body elongate or oval, ovary lies close to the testes .. 12

12. Vitellaria lie in or about the middle of body 13

Vitellaria lie in the anterior part of body 17

13. Pharynx at posterior third of body....*B. exilis* Nicoll, 1915.

Pharynx at middle of body 14

14. Excretory vesicle extending to or near about pharynx .. 15

Excretory vesicle extending much farther forward .. 16

15. Uterus extending anteriorly usually only to the anterior edge of ovary, rarely up to the anterior edge of vitellaria, cirrus sac always extending beyond posterior border of posterior testis and sometimes reaching to pharynx (at times about $\frac{1}{2}$ body length)....*B. arcuata* (Linton, 1900).

Uterus extending anteriorly between vitellaria far forward almost to the anterior sucker, cirrus sac $\frac{1}{3}$ to $\frac{1}{4}$ body length .. .. *B. longoviferus* (Manter, 1940).

16. Very elongate narrow form, cirrus sac smaller, $\frac{1}{8}$ body length, does not extend anteriorly upto posterior testis. Intestine elongate. Uterus does not extend anteriorly anterior to ovary. Gonads widely separated....., *B. microcirrus* n.sp.

Small broad and oval form, cirrus sac larger, at times being $\frac{1}{2}$ body length, always extending beyond posterior border of posterior testis and sometimes reaching to pharynx. Intestine sac-like. Uterus extends anteriorly anterior to ovary, gonads not widely separated. ..... *B. pusilla* (Stafford, 1904).

17. Cirrus sac reaching the level of testes 18

Cirrus sac not reaching upto posterior testis.....*B. elongata* Ozaki, 1928.

18. Pharynx between first and middle third of body 19

Pharynx posterior to or near mid-body 20

19. Ovary posterior to pharynx, intestine saccular.....(Type species) .. .. *B. gracilescens* (Rud., 1819).
Ovary near pharynx. Intestine elongate.....*B. ovatus* (Linton, 1900).

20. Ovary in the anterior half of the body 21
Ovary in the posterior half of the body.....*B. triglæ* (van Beneden, 1870).

21. Cirrus sac extending forward upto the level of the anterior end of the œsophagus beyond pharynx. Anterior testis is comparatively much smaller.....*B. belonea* (Srivastava, 1939).

Cirrus sac not extending beyond pharynx, testes almost equal.....*B. southwelli* (Nagaty, 1937).

GENUS .. 2. *Rhipidocotyle* Diesing, 1858.
(Syn.: *Nannœnteron* Ozaki, 1924).

(a) *Rhipidocotyle ligulum*, n.sp.

[Text-Figs. 2, 2 (*a*), 2 (*b*)]

Specimens of this gasterostome were found, in winter of 1940, in the alimentary canal of the marine fish, *Arius falcarius*. The degree of infection was poor.

Living worms are white, translucent, delicate forms covered over by mucilaginous secretion all over their body. Their vitellaria and eggs appear golden yellow in colour.

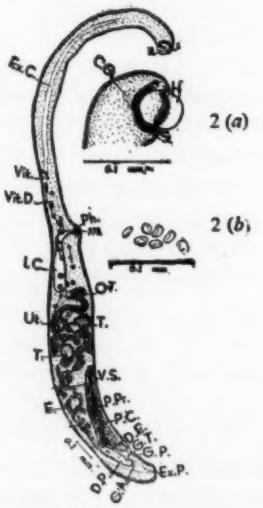

FIG. 2

Rhipidocotyle ligulum n.sp. (Lettering as in Fig. 1)

FIG. 2 (*a*) Hood (magnified) FIG. 2 (*b*) Eggs (enlarged)

Body thin, narrow and elongate. Anterior part of the body narrow, and both the extremities rounded. Most of the organs are confined to the posterior cylindrical half of the body. The anterior flat half contains a few vitellarian follicles, excretory vessel and the anterior organs of attachment. The worms assume various shapes during stages of preservation. Body is covered over with minute spines which are more numerous in the anterior region. Most of them are lost in the process of staining and mounting. Length 2·68 mm.; width 0·21 mm. (about 1/13 body length) maximum being at the level of testes. Anterior sucker (*S.*) muscular, subterminal measuring 0·12 × 0·075 mm. A prominent but feebly muscular hood or cephalic disc (*H.*) is present on the sucker. It is crescent-shaped without any papillæ and measures 0·08 × 0·03 mm. No mid-ventral notch was observed on the disc. The glandular mass of the "Cytogenous organ" (*C.G.*) is very small. Mouth (*m.*) is a small, indistinct opening situated ventrally at a distance of 1·35 mm. from the anterior end. It opens into a small compact but muscular pharynx (*Ph.*) measuring 0·04 × 0·02 mm. It is a sub-spherical structure. Oesophagus (*Oes.*) is narrow and very small; horizontal in extension, measuring about 0·03 mm. It is immediately followed by a narrow, long and very thin-walled intestine (*I.C.*) running in the antero-posterior axis. Its length is about 0·31 mm. ($\frac{1}{8}$ body length), with maximum width being in the posterior third of the organ.

Gonads spaced, situated posterior to the intestine. Ovary (*Ov.*) is elongate, pear-shaped, smooth, pre-testicular, situated in such a manner that its longer axis is horizontal, just posterior and lateral to the intestine, to its left with the tapering end pointing towards the alimentary canal. It measures 0·085 × 0·045 mm. Mehlis's gland is situated midway between the testes. Vitelline follicles (*Vit.*) large, round in outline, about 21 on the right side and 13 on the left, forming two separated, lateral, distinct, longitudinal bands extending from a distance of about 1·13 mm. from the anterior end to a distance about 0·8 mm. (right) and 0·10 mm. (left) from the posterior extremity. The number of follicles and their extension is more on the right side than on the left. The follicles on the left side start a little later and extend upto ovary; whereas those on the right extend even beyond the anterior testis. Size of the follicles varies from 0·01 to 0·03 mm. Vitelline ducts (*Vit.D.*) are distinct. Uterus (*Ut.*) is not much coiled but is heavily laden with eggs. It runs alongside the length of the animal, not extending anterior to ovary and posterior to genital atrium. It is observed from near the pointed end of the ovary running obliquely, horizontal in between the testes, by the right side of the cirrus sac and finally the feeble metraterm (*Met.*) opens into the genital atrium (*G.A.*). Eggs (*E.*) very small numerous, ovid, broadly rounded at each end measuring 0·0035 × 0·0017 mm. (average).

Testes (*T.*) two, post ovarian, separate, obliquely tandem. The anterior testis is pointed like the ovary and is situated behind it, on the left side at a distance of 0·88 mm. from it. It measures 0·07 × 0·06 mm. The posterior testis is globular, slightly smaller than the anterior, measuring 0·06 × 0·06 mm. and is situated to the right at a distance of 0·08 mm. from the anterior testis. Cirrus sac (*C.S.*) is very elongated and narrow measuring 0·53 mm. in length (1/5 body length) and 0·08 mm. in width, the maximum being in the region of genital lobes. It is situated to the left and extends anteriorly to a distance 0·09 mm. from the posterior testis and posteriorly about 0·12 mm. before the posterior end. It encloses anteriorly a small but compact longitudinally oval vesicula seminalis (*V.S.*) 0·05 × 0·02 mm. It is followed by a poorly developed long and sinuous pars prostatica (*P.Pr.*). The prostrate gland cells (*P.C.*) surrounding the pars prostatica are well developed. The genital atrium (*G.A.*) is big and contains the genetial tongue (*G.T.*) and the two more or less ventral and dorsal genital lobes or papillæ (*D.P.*). The left lobe is slender and small and the dorsal is massive in structure filling almost the whole genital sinus. Ductus ejaculatorius (*D.E.*) is a very narrow tube. Genital pore (*G.P.*) is median, ventral and is placed some distance anterior to the posterior end of the body.

Excretory system (*Ex.C.*) is tubular. The tube extends anteriorly to a distance 0·29 mm. from the anterior end and posteriorly the bladder expands in the region of the genital atrium and opens terminally on the posterior end by an excretory pore (*Ex.P.*).

This species conspicuously differs from the other species of the genus in elongated shape of the body, general topography of the organs and the structure of its cirrus sac, structure of the genital complex, extent of excretary tube and vitelline follicles. Size and number of eggs are also very characteristic.

HOST .. *Arius falcarius.*
LOCATION .. Alimentary canal.
LOCALITY .. West coast of India, Bombay.

(*b*) *Rhipidocotyle apapillosum*, n.sp.

[TEXT-FIGS. 3, 3 (*a*), 3 (*b*)]

Only two specimens of this gasterostome were found in the alimentary canal of one out of six specimens of a marine fish, *Clupea* sp., examined from the western coast of India, during the winter season of 1940. Unfortunately one of them was spoiled during staining.

The worms when alive are dull white, translucent minute forms and show a great deal of contractability. The body is hook-shaped in preserved specimen.

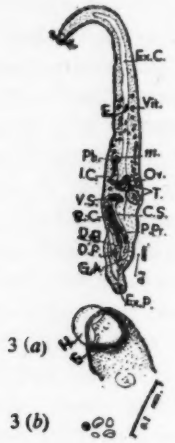

FIG. 3

Rhipidocotyle apapillosum n.sp. (Lettering as in Fig. 1)

FIG. 3 (*a*) Hood (enlarged) FIG. 3 (*b*) Eggs (enlarged)

Size of the body small, shape elongate, comparatively narrow. Its length is 1·51 mm., width 0·18 mm. (1/8 body length), maximum being in the region of the posterior testis. Anterior third of body slender, tapering and flat. The posterior two-third contains all the important organs and is cylindrical, thick and wide. The posterior end is broadly tapering round and flat. Anterior sucker (*S.*) sub-terminal, weakly muscular and measures 0·095 × 0·085 mm. Hood or cephalic disc (*H.*) in living specimens slightly wider than the anterior end of the body. It has a dorsal pad-like structure with a semi-circular anterior edge and the posterior edge is prominently notched mid-ventrally so as to divide it into two lateral lobes with rounded edges. The disc measures 0·09 × 0·06 mm. No "Cytogenous organ" was observed in this species.

Mouth (*m.*) is small and ventral situated at a distance of 0·92 mm. from the anterior end. It leads into a sucker-like, spherical pharynx measuring 0·03 mm. in diameter. Oesophagus (*Oes.*) small. Intestine (*I.C.*) saccular, extending posteriorly upto nearly the middle of the anterior testis. It measures 0·12 mm. (about 1/12 body length).

Gonads contiguous, crowded together almost at the same level. Ovary (*Ov.*) small, sub-spherical, by the left side of the intestine. It is anterior to

anterior testis and slightly overlaps it. It measures 0·05 × 0·04 mm. The vitellaria (*Vit.*) are in two, lateral, separated longitudinal groups of follicles, extending from the level of the anterior testis to a distance 0·62 mm. from anterior end. Posteriorly the follicles terminate at a distance of 0·45 mm. from the posterior end. The extent of vitelline follicles is slightly more on the left side than on the right, being 0·45 mm. on the right and 0·46 mm. on the left. The follicles are small, round and their average measurement is 0·015 mm. Their number is 14 on the right and 16 on the left side. Uterus (*Ut.*) does not extend beyond the anterior limit of vitellaria. Eggs (*E.*) are minute, few, oval in shape, ovary thin-walled, measuring 0·0125 × 0·0083 mm. (average).

Testes (*T.*) two, obliquely tandem, contiguous and oval in shape. The anterior testis is slighly smaller and is situated somewhat in the plane of mid axis of body, in the posterior region of intestine, partly below ovary, with its longitudinal axis lying horizontally. It measures 0·05 × 0·07 mm. The posterior testis is situated to the left, in contact with the anterior one, with its longitudinal axis lying in the antero-posterior direction. It measures 0·09 × 0·07 mm. Cirrus sac (*C.S.*) extends forward almost to the anterior end of the posterior testis, measuring 0·36 mm. It contains anteriorly an ovoid vesicula seminalis (*V.S.*) extending in the horizonal plane to the right of the body, measuring 0·065 × 0·03 mm. posterior to it is a long straight, somewhat poorly developed pars prostatica (*P.Pr.*) with tall prostrate gland cells (*P.C.*), opening into the genital atrium (*G.A.*) by means of ductus ejaculatorius (*D.E.*). Genital tongue (*G.T.*) is not very conspicuous, the left genital lobe or papilla is a slender fingerlike process but the right one is a big spoon-shaped papillated structure with convexity on the outer side. Genital pore (*G.P.*) is sub-terminal and inconspicuous.

Excretory vesicle (*Ex.C.*) is tubular, the bladder extending anteriorly to a distance 0·10 mm. from the anterior end. Excretory pore (*Ex.P.*) is terminal.

This species is distinguished from the other species of the genus by its smaller size, totally different general topography of the organs, extent of uterus and the size and structure of the cirrus sac.

It can be distinguished from the other species described in this paper, in the shape and size of the alimentary canal, extent of uterus, and the position of gonads. The cirrus sac is also comparatively very large in this species.

HOST .. *Clupea* sp.
LOCATION .. Alimentary canal.
LOCALITY .. West coast of India, Bombay.

(c) *Rhipidocotyle septapapillata* Krull, 1934

Some specimens of *Rhipidocotyle septapapillata* Krull, 1934, were obtained from the intestine of a marine fish, *Chrysophrys berda* from Bombay in January 1941. The specimens were very much longer than those obtained by Krull in Virginia from *Fundulus diaphanus*, the rest of the anatomy was practically identical.

The genus *Rhipidocotyle* was created by Diesing in 1858. Eckmann (1932) after a critical review of the group regards the following five as the valid species of the genus. They are *R. galeatum* (Rudolphi, 1819) type species; *R. baculum* (Linton, 1905); *R. papillosum* (Woodhead, 1929); *R. pentagonum* (Ozaki, 1924) and (?) *Gasterostomum* sp. Linton, 1910 (from *Mycteroperca bonaci*, from Tortugas, Florida); but she gives a key only to four species excluding *Gasterostomum* sp. Linton, 1910, probably because its description is inadequate.

Manter (1940 *a*) describes *Prosorhynchus atlanticus* from the same host and the same locality and thinks it as the same species as *Gasterostomum* sp., 1910. If therefore, Linton's species belongs to the genus *Prosorhynchus* it should be excluded from the genus *Rhipidocotyle*.

Since then, the following species have been added to the genus, *viz.*, *R. septapapillata* Krull, 1934; *R. transversale* Chandler, 1935; *R. elongatum* MacFarlane, 1936; *R. khalili* Nagaty, 1937; *R. eckmanni* Nagaty, 1937; *R. longleyi* Manter, 1934; *R. nagatyi* Manter, 1940; *R. barracudæ* Manter, 1940; and *R. adbaculum* Manter, 1940. Two more new species, *R. ligulum* and *R. apapillosum* have been added to the genus in this paper.

Miss F. Eckmann's (1932) key to the species of the genus has been adopted and enlarged below to include all valid species of the genus including the two described in this paper.

A Key to the Species of the Genus Rhiphidocotyle Diesing, 1858
(*Syn. Nannoenteron Ozaki*, 1924)

1. Hood or cephalic disc with papillæ 2
   Hood or cephalic disc without papillæ 7
2. The number of papillæ on the hood, 3–5 3
   The number of papillæ on the hood more than 5 5
3. The number of papillæ on the hood five 4
   The number of papillæ on the hood three....*R. khalili* (Nagaty, 1937).

4. Papillæ elongate, fine. Pharynx behind the middle of body. (Type species.) *R. galeatum* (Rudolphi, 1819).

   Papillæ-star shaped. Pharynx at or anterior to the middle of body.....*R. pentagonum* (Ozaki, 1924).

5. The number of papillæ on the hood fifteen....*R. papillosum* (Woodhead, 1929).

   The number of papillæ on the hood seven 6

6. Cirrus sac comparatively small, pear shaped, not extending anteriorly upto testes.....*R. septapapillata* Krull, 1934.

   Cirrus sac extending from anterior border of posterior testis to the posterior end of the body.....*R. longleyi* Manter, 1934.

7. Vitellaria arranged laterally in two distinct groups .. 8

   Vitellaria arranged transversely just posterior to anterior sucker ; and not separated into two distinct groups .....*R. transversale* (Chandler, 1935).

8. A conspicuous distinctly pentagonal hood or cephalic disc. 9

   Cephalic disc or hood not pentagonal 10

9. Pre-oral portion of body narrow. Vitellaria extending only to a short distance anterior to midbody. Ventral identation of cephalic disc broader, lacks markedly longitudinal coils of uterus and has larger eggs..... .....*R. barracudæ* Manter, 1940.

   Pre-oral portion of body not narrowed, vitellaria extend anteriorly to somewhat less than half-way to anterior sucker in the anterior half of the body. Coils of the uterus chiefly longitudinal.....*R. nagatyi* Manter, 1940.

10. Two sets of vitelline follicles, one on either side, occupying a central position in the third quarter of the body. .....*R. eckmanni* Nagaty, 1937.

    The vitelline glands of two sets of follicles lateral .. 11

11. Cirrus sac not reaching upto posterior testis 12

    Cirrus sac reaching upto or beyond posterior testis .. 13

12. Cephalic disc with a dorsal and two lateral lobes, vitellaria not extending posterior to pharynx, ovary and testis.

Uterine coils extend upto pharynx. Gonads in contact or not far apart. Intestine short, sac like..... .....*R. abdaculum* Manter, 1940.

Cephalic disc with no lobes. Vitellaria extend posterior to pharynx, ovary and even upto anterior testis. Gonads spaced apart. Uterine coils do not extend beyond the ovary and upto pharynx. Intestine elongated..... .....*R. ligulum* n.sp.

13. Gonads contiguous. Sirrus sac extends beyond posterior testis 14

Gonads separate, cirrus sac does not extend beyond posterior testis..... *R. elongatum* MacFarlane, 1936.

14. Larger, elongate, narrow form. Ovary situated behind pharynx, at a distance from it, vitellarian follicles 14–16, extending beyond pharynx in the anterior region to a distance about $\frac{1}{3}$ from anterior end. Anterior sucker smaller. Intestine elongate.....*R. apapillosum* n.sp.

Smaller, broad form. Ovary situated immediately behind pharynx and in contact with pharynx anteriorly and anterior testis posteriorly. Vitelline follicles ten in number and on the sides of the pharynx which is in the middle of the body ; usually not extending in the anterior half beyond pharynx. Anterior sucker comparatively bigger. Intestine saccular.....*R. baculum* (Linton, 1905).

R. ligulum and *R. apapillosum* n.spp., are the first members of the genus *Rhipidocotyle* to be described from India.

SUB-FAMILY .. 2. *Prosorhynchynchinæ* Nicoll, 1914.
GENUS .. 1. *Neidhartia* Nagaty, 1937.
Syn.: *Pseudoprosorhynchus* Yamaguti, 1938.

(a) *Neidhartia microrhyncha* n.sp.

[(TEXT-FIGS. 4, 4 (*a*), 4 (*b*), 4 (*c*) and 4 (*d*)]

Five specimens of this parasite were found in the alimentary canal of three out of seven specimens of a marine fish *Psettodes erumei* examined in the month of November 1939, at Bombay. All the organs are quite well developed except that none of the specimens contains mature eggs. Specific characters observed are so strikingly distinctive that they leave no doubt regarding the validity of the species.

The body of the parasite is very much elongate, wide and truncated, with both the extremities tapering and broadly rounded. It measures 1·39-2·93 mm. in length and 0·23-0·4 mm. in maximum width, which is in the region of pharynx and gonads. Living worms are absolutely white, thin and translucent. The cuticle is covered over by prominent triangular spines which are more closely set in the anterior region. The anterior end possesses a well-developed muscular organ, a rhynchus or rostellum (*R.*) measuring 0·144-0·23 mm. in length and 0·07–0·106 mm. in maximum width. The anterior portion of this organ is broad, pointed and is provided with two highly muscular elevated muscle bands or ridges and the posterior end is narrow and conical in shape. Internally the organ seems to possess a sheath in which it lies.

Most of the important organs of the body are confined to the posterior half of the body of the animal. Mouth (*m.*) is a simple ventral opening

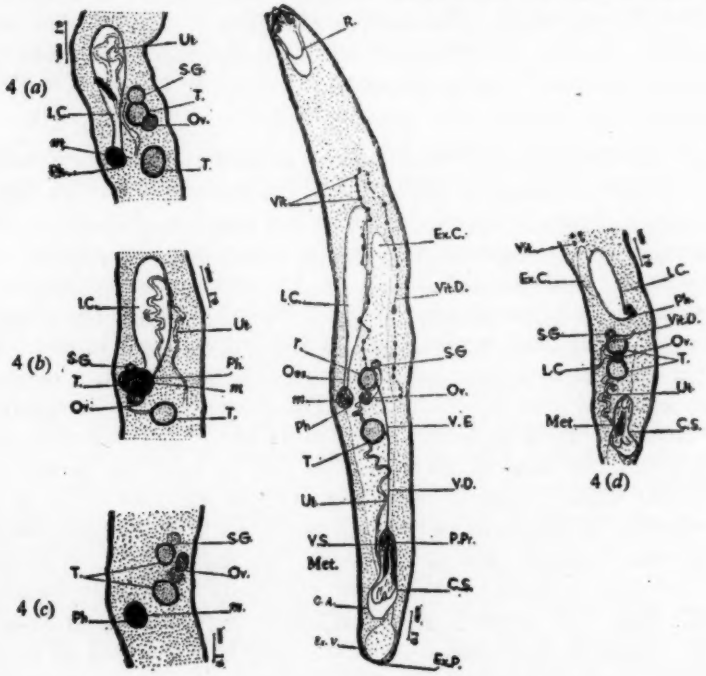

FIG. 4

Neidhartia microrhyncha n.sp.

Oes., Oesophagus ; *R.*, Rhynchus ; *V.D.*, Vas deferens ; *V.E.*, Vasa efferentia ; Other lettering as in Fig. 1.

FIG. 4 (*a*), (*b*) (*c*), and (*d*)

Variations in the relative position of gonads and digestive organs.

L.C., Laurer's canal ; other lettering as in previous figures.

situated at a distance of 0·91–1·84 mm. from the anterior end. It is followed by a small, compact, oval or globular, muscular pharynx (*Ph.*) measuring 0·06 × 0·03–0·10–0·11 mm. The position of pharynx in relation to gonads is a very variable feature. It is found that in one case (Fig. 4) it is situated at the level of the ovary, much anterior to the posterior testis and the posterior edge of the anterior testis. In the other (Fig. 4*a*) it is at the level of the posterior testis, much posterior to ovary and anterior testis. In Fig. 4*b* it is observed to be overlapping the anterior testis and ovary, anterior to posterior testis. In Fig. 4*c* it moves still forward to the posterior testis, much posterior to anterior testis and ovary. Fig. 4*d* denotes a condition where it lies completely anterior to the gonads. The position of mouth and pharynx in relation to the body and cirrus sac of the parasite is a much less variable feature. Both the pharynx and mouth are usually confined to the second third of the body and are always much anterior to cirrus sac; the distance between the two organs varying from 0·124–0·56 mm. *Oeso.* phagus (*Oes.*) is very small. The intestine (*I.C.*) has a saccular, thin-walled single cæcum, running in the antero-posterior direction. Its shape is a much variable character, being elongate to oval. It measures 0·34–0·8 mm. in length.

Gonads are always situated much anterior to the cirrus sac in or about the neighbourhood of the pharynx and mouth. The two testes (*T.*) are slightly oval or spherical bodies situated one behind the other or obliquely tandem. The anterior testis is a comparatively smaller organ than the posterior one and is situated at a distance of 0·71–1·65 mm. from anterior end. It is round in shape and measures 0·062 × 0·062–0·08 × 0·09 mm. The posterior testis is oval, larger and measures 0·075 × 0·062–0·1 × 0·12 mm. The distance between the two testes varies from 0·2 to 0·18 mm.; they are sometimes separated only by the ovary. The posterior testis is separated from the cirrus sac by a distance of 0·07–0·37 mm. The two vasa efferentia (*V.E.*) from the sides of the two testes join to form the median vas deferens (*V.D.*) which is seen to enter the vesicula seminalis (*V.S.*) in the anterior extremity of the cirrus sac. Cirrus sac (*C.S.*) is an elongated organ, situated at the posterior end of the body, to the left side. It is comparatively a small structure 1/8 to 1/9 the body length. It measures 0.175-0·33 mm. in length; the maximum width being 0·05–0·07 mm. in the region of cirrus and 0·068–0·13 mm. in the region of genital atrium (*G.A.*). Vesicula seminalis is ovoid in shape and is poorly developed. Pars prostatica (*P.Pr.*) are composed of two kidney-shaped elongate muscular lobes. Prostrate gland cells are poorly developed. The genital tongue and genital lobes or papillæ are distinct. Genital atrium or sinus

is a very prominent organ, oval in shape. It opens to the exterior subterminally on the ventral side by a distinct genital pore.

The ovary (*Ov.*) is a small oval or spherical organ, intertesticular or situated to the left of the body in the plane of cirrus sac. It is usually in continuation with the anterior testis, to its posterior side or sometimes in between the two testes. It is usually smaller than the testes and measures 0·37 × 0·37–0·08 × 0·05 mm. Shell gland (*S.G.*) is a round structure situated in continuation of the anterior testis, on its anterior side and measuring 0·031–0·06 mm. Laurer's canal (*L.C.*) is present. The vitelline glands (*Vit.*) are composed of two longitudinal strands of vitelline follicles arranged laterally one on each side, probably coming together at the anterior end. They extend forward anteriorly to a distance 0·47–0·8 mm. from the anterior end and posteriorly upto or slightly posterior to ovary. The follicles are elongately oval, granular bodies and number about 16–17 on right and 15 on the left side. Sometimes they are situated asymmetrically. The follicles are observed to extend slightly anterior to the posterior end of the intestinal cæcum; but in no case they extend upto the rhynchus. Vitelline ducts (*Vit.D.*) are clear.

The uterus (*Ut.*) consists of a few very narrow, thin coils. The coils are longitudinal in disposition and the terminal portion, metraterm (*Met.*), opens into the genital atrium. No mature ova were observed.

The excretory organ (*Ex.C.*) is a simple bladder running dorsal to the alimentary canal and terminating slightly posterior to the blind end of the intestinal cæcum. In some specimens it was also observed to extend slightly anterior to it; but it always terminates much posterior to the rhynchus. The bladder has a tendency to swell into a bulb-like swelling posteriorly and opens terminally through an excretory pore (*Ex.P.*).

The species described above possesses a rhynchus and thus belongs to the sub-family *Prosorhynchinæ* Nicoll, 1914. The genera included in this sub-family are characterised by having the anterior adhesive organ in the form of a rhynchus. The rhynchus is simple in the genus *Prosorhynchus* Odhner, 1905, and *Neidhartia* Nagaty, 1937, but is provided with tentacles in *Alcicornis* MacCallum, 1917. The rhynchus of *Mordvilkovia* Pigulewsky, 1931, has "cuticular folds" on it. The genera *Prosorhynchus* Odhner, 1905, and *Neidhartia* Nagaty, 1937, can be distinguished from each other by the position of the ovary. *Neidhartia* further differs from all the other genera included in the sub-family except *Dollfustrema* Eckmann, 1932, in having the ovary intertesticular at opposite side of testes, on the left side. The rest of them have it anterior to the anterior testis on

the right side. *Dollfustrema* differs from *Neidhartia* in the anterior end being provided with a triple-row, ring of large spines.

The new species described above under this subfamily belongs to the genus *Neidhartia* Nagaty, 1937. The genus was created by Nagaty in 1937 to include his two new species *N. neidharti* Nagaty, 1937, and *N. ghardagæ* Nagaty, 1937. Manter (1940) observes that the genus *Pseudoprosorhynchus* Yamaguti, 1938, seems to be a synonym of *Neidhartia*. This genus was created by Yamaguti in 1938, to accommodate his new species *P. synodi* from the small intestine of *Synodus japonicus*.

The two species of Nagaty are from the same host and the same locality. Their anatomy is also not very much different. Perhaps they may prove to be identical on further study.

The new species differs from the two species of the genus in the very elongate form of the body, relatively small size of the rhynchus and cirrus sac; the dilation of the excretory bladder near the posterior end and more anterior position of pharynx and gonads. The number of vitelline follicles is much more and they also do not extend to the rhynchus. The intestinal sac also extends much anterior to the anterior testis, in the anterior part of the body. The cirrus sac is 1/3 body length in Nagaty's specimens, but in the present species it is much smalller, only 1/8 to 1/9 body length and its anterior part is not closely related to the beginning of the alimentary canal, the posterior testis and the ovary. Excretory bladder is comparatively a small structure.

HOST .. *Psettodes erumei.*
LOCATION .. Alimentary canal.
LOCALITY .. West coast of India, Bombay.

(*b*) *Neidhartia neidharti* Nagaty, 1937

A single specimen of this parasite was obtained from the small intestine of a marine fish, *Belone* sp. in December 1939, at Bombay. The rhynchus of this specimen is comparatively smaller than that of Nagaty's specimen. The rest of the internal anatomy of the worm is practically identical.

It is for the first time that species of this genus also are being recorded from India.

GENUS .. 2. *Prosorhynchus* Odhner, 1905.

(Syn.: *Gotonius* Ozaki, 1924: *Skrajabiniella* Issaitschikow, 1928.)

***Prosorhynchus* sp.**

A few specimens belonging to this genus were obtained from a marine fish, *Serranus lanceolatus*, from the west coast of India, in 1940. Specific identity could not be established owing to bad state of preservation of the material.

8. Acknowledgements

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CYTOLOGICAL STUDIES IN THE FAMILY ZINGIBERACEÆ WITH SPECIAL REFERENCE TO CHROMOSOME NUMBER AND CYTO-TAXONOMY

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I. Introduction

The family Zingiberaceæ, according to Willis (1931), contains 45 genera and about 800 species. A few like *Globba*, *Amomum*, *Alpinia*, *Curcuma*, *Costus* and *Elettaria*, have come in for some investigation at the hands of the morphologists, especially in respect of the nature of the labellum. However, cytological information that is available is very meagre. The chromosome numbers known so far in this family are confined only to 11 species spread over 7 genera, as per list given below. This paucity of information on the cytology of this family has also been pointed out by Tischler (1937). It was mainly with a view to fill up ' the great gaps in our knowledge of the chromosome numbers ' of some of the families referred to by Tischler, that the present investigation was taken up. Attention has been paid mainly to the chromosome numbers, while other cytological details, like chromosome morphology and nucleolar behaviour have been described only in a few cases. A brief discussion regarding the course of evolution in this family, with the data on hand, has also been attempted.

	Genus and species	Chromosome numbers			
		n	2*n*	*Author*	*year*
1.	*Curcuma longa* Linn.		64	Sugiura	1936
2.	*Zingiber officinale* Rosc. ..		22	„	1928
	Zingiber officinale Rosc. ..		24	Takahashi	1930
3.	*Zingiber Mioga* Rosc.		55?	Morinaga *et al.*	1929
4.	*Phæomeria atropurpurea* ..	24		Boehm	1931
5.	*Costus cylindricus*	8		„	1931
6.	*Costus malarotiensis*		18	Gregory	1936
7.	*Costus speciosus*	18	36	Banerjee	1940
8.	*Elettaria Cardamomum* Maton. ..	24	48	Gregory	1936
9.	*Hedychium Elwesi* Baker ..		66	„	1936
10.	*Alpinia calcarata* Rosc.		48	Raghavan and Venkatasubban	1941

II. Materials and Methods

Materials for the present study were obtained from the Royal Botanic Gardens, Sibpur, Government Garden, Bangalore and Soundarya Nursery, Madras. *Costus speciosus* was collected from Tenmalai forests. We are indebted to Dr. S. K. Mukerjee of the Royal Botanic Garden, Sibpur, for help in the matter of identification. In the present investigation, chromosome numbers have been determined, most of them for the first time, from somatic metaphase plates. Root tips were fixed in Navashin's fluid for a period of 24 hours. After the usual process of washing, dehydration and infiltration, sections were cut at a thickness ranging from 14–18 microns and stained in Newton's Iodine-Genetian-Violet.

The following are the numbers determined in the present study :—

	2*n*		2*n*
1. *Zingiber officinale* Rosc. ..	22	14. *Alpinia galanga* Sw. obs. ..	48
2. *Zingiber cassumunar* ..	22	15. *Alpinia nutans* Rosc. ..	48
3. *Zingiber zerumbet* Sm. ..	22	16. *Alpinia vittata* Bull. ..	48
4. *Curcuma aromatica* Salisb.	42	17. *Alpinia allughas* Rosc. ..	48
5. *Curcuma longa* Linn. ..	62	18. *Globba bulbifera* ..	48
6. *Curcuma amada* Roxb. ..	42	19. *Hedychium flavescens* Cau.	34
7. *Kæmpferia Gibsoni* ..	24	20. *Hedychium Greenii* ..	36
8. *Kæmpferia Gilbertii* Bull. ..	36	22. *Hedychium flavum* Roxb. ..	52
9. *Kæmpferia rotunda* Linn. ..	54	23. *Hedychium coronarium* Koenig. ..	54
10. *Kæmpferia Galanga* Linn. ..	54	24. *Hedychium Gardnerianum* Rosc. ..	54
11. *Costus igneus* N.E.Br. ..	18	25. *Hedychium gracile* Roxb. ..	66
12. *Costus discolor* ..	18		
13. *Costus speciosus* Smith. ..	36		

III. Observations

The nature of the chromosomes with reference to their morphology, could not be studied for all the species investigated, on account of their small size and comparatively large number. However, an analysis of the chromosome complements has been made for two species of *Costus* (*C. igneus* and *C. discolor*) and three species of *Zingiber*, namely, *Z. officinale*, *Z. cassumunar* and *Z. zerumbet*.

The chromosome number for *Costus igneus* is $2n = 18$ (Text-Fig. 1). Among the chromosomes, there is not much disparity of size. Almost all of them show a median attachment constriction, except the pairs AA and BB which show a subterminal constriction (Text-Fig. 2). Out of the 9 pairs, 6 are rod-shaped while the remaining are crescent-shaped.

Costus discolor reveals the presence of $2n = 18$ chromosomes (Text-Fig. 3), as in *C. igneus*. Here also, there is a preponderance of the rod-shaped chromosomes over the crescent-shaped ones. There are 6 pairs of rods and 3 pairs of crescent-shaped chromosomes as in *C. igneus*. Of the 6 pairs of rod-shaped chromosomes, one pair alone (A′A′, Text-Fig. 4), shows the presence of subterminal constriction. It may be mentioned that this pair A′A′ is the smallest of the lot. The rest of the chromosomes, both rods and crescents, exhibit median or submedian attachment constriction. The chromosome morphology in the two species described above, is quite similar, as can be seen from their idiograms (Text-Figs. 2 and 4). In both the species, no SAT-chromosomes could be observed.

Costus speciosus shows $2n = 36$ chromosomes (Text-Fig. 5). One of the chromosomes exhibits a trabant.

All the three species of *Zingiber* examined, namely, *Z. officinale*, *Z. zerumbet* and *Z. cassumunar*, have the same chromosome number $2n = 22$. The somatic metaphase plates of these are illustrated in Text-Figs. 6, 7 and 8. Text-Fis. 9, 10 and 11 represent their respective

idiograms. Though the chromosome number happens to be the same in all the three species, there are differences in their morphology. The chromosomes of *Z. officinale* are somewhat thin and slender, compared to those of the other two species. The chromosomes can be classified into long, medium and short on the basis of their lengths, although the difference between the long and the medium is not very striking. Classified on this

basis, the chrosmosomes can be grouped into 5 long, 4 medium and 2 short pairs. From the point of view of shape, there are 6 pairs of 'rods' (of these 2 pairs belong to the long chromosomes and the rest to the medium), 3 pairs—G'G', H'H' and I'I' (Text-Fig. 9), taking the configuration of the letter V (these belong to the category of long chromosomes) and 2 pairs of 'crescents'. The 2 pairs of 'crescents' are the shortest of the lot, as can be seen in Text-Fig. 9. All the chromosomes exhibit either sub-median or median constriction.

In *Z. cassumunar* (Text-Figs. 8 and 11), there are 11 pairs of somatic chromosomes. The chromosomes are fairly stout and comparable in diameter to those of the species of *Costus* examined. In almost all these, median or submedian constrictions are exhibited, except the pairs A'A' and I'I' (Text-Fig. 11). These two pairs have a subterminal kinetochore. Of the 11 pairs of chromosomes, 7 are of the rod-type. Of the remaining 4 pairs, G'G' and H'H' (Text-Fig. 11), take the configuration of the letter V, while the rest of the pairs are short chromosomes of the crescent-type with median constriction. The pair H'H' (Text-Fig. 11) represents the longest chromosomes in the complement. Of the 3 pairs of short chromosomes, only the pair I'I' (Text-Fig. 11) exhibits subterminal constriction, the rest showing a median constriction. No trabants could be observed though several plates were examined.

Zingiber zerumbet.—The somatic number in this species is 22 (Text-Fig. 7). There is a striking similarity in chromosome morphology to that of *Z. cassumunar*. This can be seen by comparing their respective idiograms in Text-Figs. 10 and 11. There is one pair E'E' (Text-Fig. 10) in which one chromosome shows the presence of a satellite at its proximal end. The satellite in its homologue, could not, however, be observed.

A comparison of the idiograms of the 3 species of *Zingiber* studied (Text-Figs. 9, 10 and 11), would show that the chromosomes of *Z. officinale* are different from the rest, not only in respect of their slender nature, but in their morphology also. In *Zingiber offcinale*, there are 3 long pairs of V-shaped chromosomes, while in *Z. zerumbet* and *Z. cassumunar*, there are only 2 such pairs of chromosomes. In *Z. officinale*, there are only 2 pairs of short chromosomes (both the pair showing median constriction) while in *Z. zerumbet* and *Z. cassumunar*, there are 3 pairs of short chromosomes (2 pairs of crescents with median constriction and a pair of rod exhibiting sub-terminal constriction). On the other hand, as has been pointed out previously, the chromosome morphology of *Z. zerumbet* and *Z. cassumunar* are almost identical as can be seen in Text-Figs. 10 and 11.

Three species of *Curcuma* have been included in the present study. Of these, *Curcuma aromatica* and *Curcuma amada* (Text-Figs. 12 and 13), each shows $2n = 42$ chromosomes. *Curcuma longa* (Text-Fig. 14), on the other hand, exhibits $2n = 62$ chromosomes. More than a dozen good plates were examined for confirmation of counts. Sugiura (1936) has, however, given $2n = 64$ as the number for the same species. The chromosomes of all the three species of *Curcuma* are very small, compared to those of the *Zingiber* species examined. These are rod-shaped with sub-median or sub-terminal centromeres. All the three species resemble one another in the general appearance of their chromosomes.

Four species of *Kæmpferia* were studied, namely, *K. Gibsoni* ($2n = 24$, Text-Fig. 15), *K. Gilbertii* ($2n = 36$, Text-Fig. 16), *K. rotunda* ($2n = 54$, Text-Fig. 17) and *K. Galanga* ($2n = 54$, Text-Fig. 18). The chromosomes in all these are fairly alike and their number conform to a regular polyploid series, all of them being multiples of 6. In *K. Gibsoni*, 2 chromosomes with sub-terminal constriction exhibit the presence of trabants (Text-Fig. 15). A pair of SAT-chromosomes is also seen in *K. rotunda* (Text-Fig. 17).

The four species of *Alpinia* investigated, show the same chromosome number, $2n = 48$. The somatic metaphase plates of these are illustrated in Text-Figs. 19, 20, 21 and 22. The chromosomes show a broad similarity in configuration, not only among the four species examined, but also to those of *Curcuma* and *Hedychium*. It appears that prochromosomes are a special feature of this genus. A detailed study of the nature and behaviour of these bodies has been made already, by Raghavan and Venkatasubban (1941), in *Alpinia calcarata*. In *Alpinia allughas*, the attachment of 4 prochromosomes to a single nucleolus (Text-Fig. 23), has been noticed at the prophase of somatic mitosis. Sometimes 4 nucleoli, instead of a single nucleolus could be recognized at early prophase (Text-Fig. 24). Of these 4 nucleoli, one is exceptionally big, while the rest are small and are similar. It is interesting to record that corresponding to this big nucleolus, there is one big prochromosome attached to the nucleolus as can be seen in Text-Figs. 23 and 24.

Hedychium flavescens shows $2n = 34$ chromosomes (Text-Fig. 25). *Hedychium Greenii* exhibits $2n = 36$ (Text-Fig. 26), *H. flavum* $2n = 52$ (Text-Fig. 27), *H. Gardnerianum* and *H. coronarium* (Text-Figs. 28 and 29) each exhibits $2n = 54$, while *H. gracile* (Text-Fig. 30) shows $2n = 66$ chromosomes. The chromosome size and general appearance in all these species are more or less alike, except in *H. gracile* where the number of small chromosomes is very large. In *H. flavescens*, prochromosomes were seen just as in the species of *Alpinia*. Text-Fig. 31 shows 4 prochromosomes attached to

a single nucleolus at the early prophase of somatic mitosis. As in *Alpinia allughas*, occasionally 4 nucleoli are recognizable at early prophase (Text-Fig. 32). Of these, two are big and the remaining ones small. Obviously, all these are cases of delayed fusion of the nucleolar bodies. Normally, the nucleoli that are organized at telophase, undergo fusion into a single large body almost immediately. But in such cases as these, the fusion has been presumably delayed. In *Hedychium flavum* also, there are found 4 nucleoli at early prophase (Text-Fig. 33). In *H. Greenii*, stray tetraploid cells were met with in the region of the periblem. Chromosome counts made from such cells, corroborate that the $2n$ number for this species is 36. A diploid and a tetraploid cell are shown in Text-Figs. 34 and 35. From these two figures, it could be seen that the tetraploid cell is approximately twice as big as the diploid cell. The same is the case with the diploid and tetraploid nuclei also.

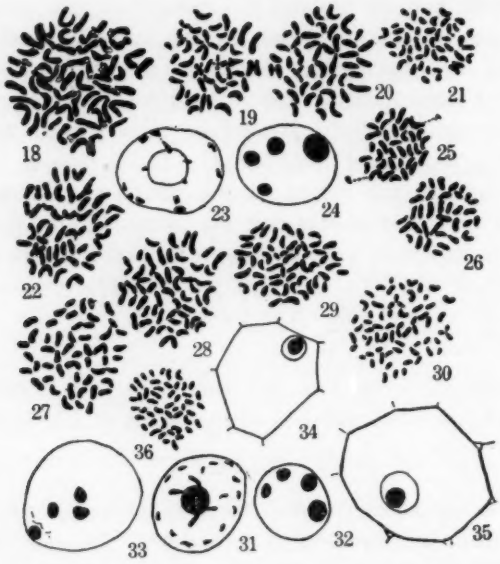
Globba bulbifera (Text-Fig. 36) shows $2n = 48$ chromosomes. The chromosomes are short and rod-like as in species of *Curcuma*.

IV. Discussion

(*a*) *Chromosome numbers in relation to taxonomy.*—The increasingly important role that chromosome numbers and chromosome morphology play in the realm of plant taxonomy, has in recent years been emphasized by various workers, investigating different plant families and genera. These investigations have revealed in an unmistakable manner, the significance of chromosome numbers in plant taxonomy. Chromosome number, chromosome morphology and other cytological data, have often given decisive evidence on disputed taxonomical questions. Thus, for example, the position of the genus *Brunnera* in the *Boragineæ*, has been the subject of controversy among taxonomists. Some hold (Johnston, 1924), that it well merits a generic distinction, while others relegate it to the position of a species of *Anchusa*. Smith's (1932) investigation on the cytology of this genus confirmed Johnston's findings, namely, that it was a distinct genus. Another interesting discovery along these lines is provided by the genera *Yucca* and *Agave*. McKelvey and Sax (1933) found that *Yucca*, *Agave* and some related genera had identical chromosome complements; so distinctive were they, that it was unthinkable, that the complements could have arisen independently in both the Liliaceæ and Amaryllidaceæ. In this case therefore, cytology offers a strong evidence in support of Hutchinson's (1934) treatment of these genera as a distinctive family Agavaceæ.

Much cytological data are yet to come, before they can be employed effectively and decisively in the field of taxonomy. But even with the

relatively meagre and incomplete data already at hand, there are a number of well-known instances where cytological data have been employed as a useful



guide to taxonomic relationships. Smith (1933) has discussed the cytological evidence obtained by Bruun (1932) for the genus *Primula*, in the light of his own taxonomic studies in that genus. He concludes that "the contribution (of the Cytologists) has been of the greatest interest and value; but only by marshalling *all* the data, morphological and cytological, can a final judgement be made". An attempt on these lines was made by Raghavan and Rangaswamy (1941) in respect of the family Rubiaceæ and also in the family Aizoaceæ (Raghavan and Srinivasan, 1940). In these, both morphological and cytological data were employed for the elucidation of the problem of the evolution of the genera within the respective families.

A rather elaborate cytological investigation of about 40 members of the family Bignoniaceæ has led Venkatasubban (1943) to formulate a tentative scheme of the phylogenetic relationship of the different genera within the family.

The Geraniales have been considered by Warburg (1938) from the same cyto-taxonomical point of view.

Other investigations relating to the evolution of species in particular genera, are those of Baldwin (1938) for the genus *Kalanchæ*, Anderson and

Sax (1936), for the American species of Tradescantia, Babcock and Cameron (1934), for the genus *Crepis*. Anderson (1937) and Kostoff (1939) have discussed this problem in some detail.

In some cases, however, chromosome numbers and morphology have failed to yield any clue as regards speciation within a genus. Such is the case of the genus *Lathyrus*, where Senn (1938), found identical chromosome number and morphology in all the species thereof, which he investigated. The genus *Crotalaria* would also appear to belong to this category, since the few species investigated (*Crotalaria usorensis* $n = 8$, *C. laburnifolia* $n = 8$, *C. breviflora* $n = 8$, *C. verrucosa* $n = 8$ and *C. lanceolata* $n = 8$) all show the same chromosome number and morphology (Raghavan and Venkatasubban, unpublished work).

In the present investigation, mainly chromosome numbers alone have been employed for the elucidation of the problem of the evolution of the different genera within the family Zingiberaceæ. Though, chromosome numbers of over 25 species spread over 7 genera have been determined, mostly for the first time, the list is by no means complete and as such the scheme presented must be regarded as a tentative one, drawn with the help of all available cytological data. Further information that might come in the future years would show whether or not the present inferences have to be modified.

The chromosome numbers known so far in this family, are restricted to 33 species (including the 25 species of the present investigation) spread over 9 genera. These may now be examined from the point of view of their basic numbers.

All the three species of *Zingiber* examined show $2n = 22$. The morphology of the chromosomes has already been described. *Z. Mioga* is reported to show $2n = 55$ (Morinaga, *et al.*, 1929). It is very probable, that the different species of *Zingiber* are diploids with 11 as the basic number. Some evidence for this could be gained from the occurrence of a SAT-chromosome in one of the pairs in the somatic complement of *Z. zerumbet*.

In the genus *Curcuma*, the following numbers are met with. *C. aromatica* and *C. amada*, $2n = 42$ and *C. longa*, $2n = 62$. According to Sugiura (1936), *C. longa* has a somatic complement of 64 chromosomes. However, the local material of *C. longa*, which we examined showed only $2n = 62$, in the several metaphase plates examined. *C. longa* is likely to have arisen by a process of triploidy, either from *C. aromatica* or a form closely similar to it with 42 chromosomes. This suggestion is made since morphologically the two species are alike, except for the aromatic smell of the

rhizome of *C. aromatica*. If it is a triploid of a 42-chromosomed type, it ought to show $2n = 63$. But such a form would be unstable, due to the presence of an odd chromosome. Stability can however be secured either by the elimination or duplication of the odd chromosome. Therefore, the stable forms will exhibit either $2n = 62$ or $2n = 64$ chromosomes as the case may be. These numbers have actually been met with in the present investigation ($2n = 62$), and in the count made by Sugiura (1936, $2n = 64$). The culture of *C. longa*, in our Botanical Garden, unfortunately would not flower, though several plants were raised from rhizomes. Only the meiotic behaviour of the chromosomes would throw light as to whether it is a triploid and if so the nature of the triploidy. It is interesting to note that on the whole, the configuration of the chromosomes in the complements of the three species, would appear to be almost identical. This would indicate that the 42-chromosomed species must have got differentiated, by structural changes of the chromosomes rather than changes in morphology. The basic number of this genus would thus appear to be 21.

The four species of *Kæmpferia* examined, show a regular polyploid series—24, 36 and 54, all multiples of 6. It is likely that 6 is the basic number for this genus. The size of the chromosomes is more or less the same in *K. Gibsonii* ($2n = 24$), *K. Gilbertii* ($2n = 36$), *K. rotunda* ($2n = 54$) and *K. Galanga* ($2 = 54$). Therefore, increase in the chromosome number in this genus, has not been attended by any diminution in the size of the chromosomes.

In the genus *Costus*, the available numbers are $2n = 18$ for *C. malarotiensis*, *C. igneus* and *C. discolor;* $2n = 36$ for *Costus speciosus* and $2n = 16$ for *C. cylindricus*. It would be seen that barring *C. cylindricus* ($2n = 16$, Boehm, 1931), all the others conform to the 9-series. It is, therefore, suggested that 9 is likely to be the basic number of this genus.

The different species of *Alpinia* investigated exhibit the same chromosome number $2n = 48$. This number is likely to have resulted from a basic number 12. In other words, *Alpinia* species with $2n = 48$ chromosomes, are likely to be tetraploids. Support for this can be gathered from other data also. In *Alpinia allughas* (Text-Fig. 23), 4 prochromosomes were frequently found attached to a single nucleolus. These are obviously the nucleolar chromosomes. Further, in the somatic telophase and prophase, 4 nucleoli were found to be organized (Text-Fig. 24). A similar case of attachment of 4 prochromosomes to a single large nucleolus and the organization of 4 nucleoli at somatic telophase, have been figured and described by Raghavan and Venkatasubban (1941) for *Alpinia calcarata*.

Such evidences though not conclusive by themselves, can still throw light regarding the ploidy of the species, if considered in conjunction with other data.

Globba bulbifera, *Elettaria Cardamomum* and *Phæomeria atropurpurea* agree in their chromosome number ($2n = 48$) and general appearance. It is therefore likely that these are related genera, not only to one another but also to the genus *Alpinia*. All these genera are likely to have been evolved from the basic number 12.

In the genus *Hedychium*, there appears to be a wide range of variation in the chromosome number. *H. flavescens* exhibits $2n = 34$, *H. Greeni* $2n = 36$, *H. flavum* $2n = 52$, *H. coronarium* $2n = 54$, *H. Gardnerianum* $2n = 54$, *H. gracile* $2n = 66$ and the same number for *H. Elwesi* (Gregory, 1936). The chromosomes in all these species, fairly agree with reference to their size and morphology, though no detailed study could be made in this direction. *H. flavescens* ($2n = 34$), shows also the attachment of 4 prochromosomes to a single nucleolus and 4 nucleoli at the somatic prophase as can be seen from Text-Figs. 31 and 32. From these, it would appear that this species is likely to be a tetraploid, from a 9-chromosomed form. The number 34 could have been derived from 36, either by elimination of a pair of chromosomes or end-to-end fusion of two pairs of chromosomes. Reference to Text-Fig. 25 would show two chromosomes, A and B, somewhat longer than the rest. These are likely to have arisen by such an end-to-end fusion. Similar end-to-end fusion of the chromosomes has been recorded by Davie (1933), in the different genera of Malvaceæ. Therefore the basic number for species having $2n = 36$, $2n = 34$ chromosomes is likely to be 9. The 54-chromosomed forms like *H. coronarium* and *H. Gardnerianum* may, at first sight, appear to be hexaploids from the basic number 9. But details of nucleolar organization would appear to point out to their being tetraploids rather than hexaploids. For, *H. flavum* ($2n = 52$) reveals the presence of 4 nucleoli at somatic telophase and hence must be regarded as a tetraploid. The basic number from which this tetraploid form could be derived is likely to be 13. By the duplication and reduplication of the entire genom of this ancestral form with 13 chromosomes, a species with 52 chromosomes could be obtained. From the number 52, the number 54 exhibited by *H. coronarium* and *H. Gardnerianum*, could be derived by the duplication of a pair of chromosomes. *H. gracile* and *H. Elwesi* can be regarded as hyperpentaploid from this basic number 13. It would thus appear that speciation in the genus *Hedychium* has evolved along the 9 series and the 13 series. It is noteworthy that side by side with polyploidy, aneuploidy also has been responsible for the evolution of the species along both the lines.

(*b*) *Some Phylogenetic Considerations*.—Loesner in Engler and Prantl, *Pflanzenfamilien*, edition 2, divided the family Zingiberaceæ into two subfamilies, Zingiberoideæ and Costoideæ. The same classification has also been adopted by Rendle (1930). Hutchinson (1934) on the other hand considers these as mere tribes. Thus according to him, there are 4 tribes constituting this family. These are *Costeæ*, *Hedychieæ*, *Globbeæ* and *Zingibereæ*.

The tribe *Costeæ* consists of 4 genera, *Costus*, *Monocostus*, *Dimerocostus* and *Tapeinochilus* (Hutchinson, 1934). There are about 110 species and 92 of these belong to the genus *Costus* (Rendle, 1930). The 6 species of *Costus*, for which chromosome numbers are available, all show $2n = 18$, or $2n = 36$ except *C. cylindricus*, which alone is reported to show $2n = 16$ (Boehn, 1931). The basic number for this genus has been indicated to be 9. The chromosomes are quite distinctive in their appearance and morphology and are different from the rest of the genera examined. Therefore the existence of the tribe Costeæ is quite justifiable on the ground of chromosome number and chromosome morphology.

In the tribe Hedychieæ, there are 14 genera and about 200 species (Rendle, 1930). But according to Hutchinson (1934) there are 16 genera. Chromosome numbers are available only for 3 genera and 16 species. The numbers range from 34 to 66 for the 8 species of *Hedychium* examined. It has been suggested already that these species are likely to have been evolved, one along the 9 series and the other along the 13 series. The occurrence of more than one basic number for a genus is not unusual. According to Babcock and Cameron (1934), the genus *Crepis* has several basic numbers. The genus *Hedychium* appears to be a recently evolved one. This inference is drawn from the chromosome numbers in the different species being variable. The 4 species of *Kæmpferia* examined show a regular polyploid series. The chromosome number in these are multiples of the basic number for this genus namely 6. It has been suggested previously that 21 is the basic number for the genus *Curcuma*. This number can be obtained by a process of amphidiploidy. If two forms with 12 and 9 haploid chromosomes each, had undergone a natural cross, the resulting form might have given rise to a plant with 21 chromosomes. From such a stock, the 42 and 62 chromosomed forms can easily be derived, by a process of duplication. There is a good deal of evidence to show that amphidiploidy has played an important role in the evolution of new forms. For example, Huskins (1931), has shown that *Spartina Townesendii* (126 chromosomes), is likely to be an amphidiploid derived from *Spartina stricta* (56 chromosomes) and *Spartina alterniflora*

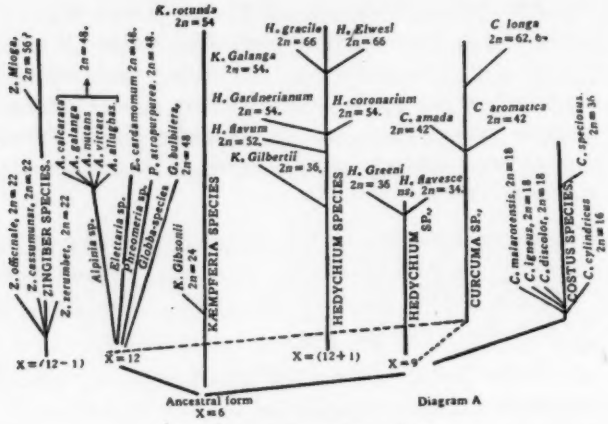
(70 chromosomes). Again, Anderson (1936) has shown that *Iris versicolor* (108 chromosomes) has been derived from *Iris setosa* (38 chromosomes) and *Iris virginica* (70 chromosomes). Interesting cases of amphidiploidy have been described in the genus *Pentstemon* by Keck (1932) and Clausen (1933). The same phenomenon has also played a role in the evolution of some species of *Crepis* (Babcock and Cameron, 1934) and also in the genus *Kalanchæ* (Baldwin, 1938).

The tribe *Globbeæ* according to Hutchinson (1934), consists of 4 genera, *Globba*, *Hemiorchis*, *Gagnepainia* and *Mantisia*. Chromosome number is available only for *Globba bulbifera* ($2n = 48$). This genus is likely to have arisen from a basic number 12.

Lastly the tribe *Zingibereæ* has 20 genera and 350 species (Rendle, 1930). Chromosome numbers are available for only 4 genera and 11 species. The basic number for *Zingiber* appears to be 11 while for genera like *Alpinia*, *Elettaria* and *Phæomeria*, 12.

Thus the prevailing basic numbers of the different genera are 6, 9, 11, 12, 13 and 21. Of these 6 may be regarded as the primary basic number from which other basic numbers have arisen secondarily. In the course of evolution of the different genera and species, polyploidy seems to have played an important role. It is suggested that the existing forms of *Curcuma* species are amphidiploids derived from a cross between 12-chromosomed and 9-chromosomed ancestors. The genus *Hedychium* is a recently evolved one—an inference drawn from the chromosome numbers in the different species being variable. Polyploidy and aneuploidy have played their parts in the evolution of the different species in this genus. A biphyletic origin is also suggested for this genus, one from the basic number 9 and another from the basic number 13. The genus *Alpinia* is characterized by its extreme stability as in all the different species examined the chromosome number has been found to be $2n = 48$. This is likely to be a very old genus. From the point of view of chromosome morphology, the genus *Costus* warrants a distinction into a tribe or sub-family. The same may be said of the genus *Zingiber* also while the rest of the genera like *Alpinia*, *Elettaria*, *Globba*, *Hedychium* may be clubbed together into a tribe. This is suggested in view of the fact that the chromosome number and chromosome morphology are almost identical in these genera.

The conclusions drawn in the previous pages have been represented schematically in Diagram A.



V. Summary

Somatic chromosome numbers have been determined mostly for the first time for 24 species, spread over 7 genera.

Chromosome complements in *Zingiber officinale*, *Z. zerumbet*, *Z. cassumunar*, *Costus igneus* and *C. discolor* have been analysed.

The basic numbers 6, 9, 11, 12, 13 and 21 are suggested for the genera *Kæmpferia*, *Costus*, *Zingiber*, *Alpinia*, *Hedychium*, *Elettaria*, *Globba* and *Phæomeria*. 6 appears to be the primary basic number, the others representing secondary balances of this primary number.

A biphyletic origin is suggested for the species of *Hedychium* one from the basic number 9 and the other from the basic number 13.

Speciation in this family has been found to be due to polyploidy, aneuploidy and structural changes.

The 42 chromosomed members of the genus *Curcuma* are believed to be amphidiploids derived from a cross between 12- and 9-chromosomed ancestors. It is also suggested that *Curcuma longa* is likely to be a triploid form of *C. aromatica*.

The distinctive nature of the chromosomes of *Costus*, their morphology and number, would appear to justify the separation of this genus into a tribe or sub-order.

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LEGEND TO TEXT-FIGURES 1–36

(All figures have been drawn with a camera lucida at an approximate magnification of ×3600 except figures 34 and 35 which are approximately × 1200.)

TEXT-FIG.

1. Somatic metaphase plate of *Costus igneus* ($2n = 18$).
2. Idiogram analysis of *Costus igneus*.
3. Somatic metaphase plate of *Costus discolor* ($2n = 18$).
4. Idiogram of *Costus discolor*.

5. Somatic metaphase plate of *Costus speciosus* ($2n = 36$).
6. Somatic metaphase plate of *Zingiber officinale* showing $2n = 22$.
7. Somatic metaphase plate of *Z. zerumbet*. One of the chromosomes shows a trabant ($2n = 22$).
8. Somatic metaphase plate of *Z. cassumunar*, $2n = 22$.
9. Idiogram of *Zingiber officinale*; note the presence of 3 pairs G'G', H'H' and I'I' of V-shaped configuration.
10. Idiogram of *Z. zerumbet*; one of the chromosomes of the pair E'E' showing a satellite. There are only 2 pairs of V-shaped chromosomes.
11. Idiogram of *Z. cassumunar*; There are 2 pairs of V-shaped chromosomes—G'G' and H'H'. The pair A'A' and I'I' show subterminal constriction.
12. Somatic metaphase plate of *Curcuma aromatica* showing $2n = 42$ chromosomes.
13. „ „ *Curcuma amada* ($2n = 42$).
14. „ „ *Curcuma longa* ($2n = 62$).
15. „ „ *Kæmpferia Gibsonii*, $2n = 24$; 2 of the chromosomes show satellite.
16. „ „ *Kæmpferia Gilbertii*, $2n = 36$.
17. „ „ *Kæmpferia rotunda*, $2n = 54$.
18. „ „ *Kæmpferia Galanga*, $2n = 54$.
19. „ „ *Alpinia galanga*, $2n = 48$.
20. Somatic metaphase plate of *Alpinia nutans*, $2n = 48$.
21. „ „ *Alpinia vittata*, $2n = 48$.
22. „ „ *Alpinia allughas*, $2n = 48$.
23. Late somatic telophase of *Alpinia allughas* showing the attachment of 4 prochromosomes attached to a single nucleolus. One of the prochromosomes is bigger than the rest.
24. Early prophase of somatic mitosis of *Alpinia allughas*, showing the presence of 4 nucleoli of which one is bigger than the rest.
25. Somatic mataphase plate of *Hedychium flavescens*, $2n = 34$. The chromosomes A and B are somewhat bigger than the rest and are likely to have been formed by a process of end-to-end fusion.
26. Somatic metaphase of *Hedychium Greeni*, $2n = 36$.
27. „ „ *H. flavum*, $2n = 52$.
28. „ „ *H. Gardneranium*, $2n = 54$.
29. „ „ *H. coronarium*, $2n = 54$.
30. „ „ *H. gracile*, $2n = 66$.
31. Somatic telophase of *Hedychium flavescens* showing the attachment of 4 prochromosomes.
32. Somatic prophase of *H. flavescens* showing 4 nucleoli.
33. „ „ *H. flavum* showing 4 nucleoli.
34. A diploid cell of *H. Greenii* from the periblem of root tip. × 1200.
35. A tetraploid cell of *H. Greenii* from the periblem or root tip. × 1200.
36. Somatic metaphase plate of *Globba bulbifera*, $2n = 48$.

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TREMATODES FROM INDIAN MARINE FISHES

Part III. Description of a New Species of the Genus *Mehratrema* (Family *Monodhelminthidae* Dollfus, 1937)

By B. S. Chauhan

(*College of Science, Nagpur, India*)

Received April 7, 1943

(Communicated by Dr. M. A. Moghe, F.A.SC.)

Numerous specimens of this distome belonging to the genus *Mehratrema* Srivastava, 1939, of the family *Monodhelminthidæ* Dollfus, 1937, were found in the intestines of the marine fishes *Polynemus indicus*, *Muræsox talabonoides*, and *Sciæna* sp. at Bombay. The former two were examined in the winter season in 1940 and the latter in the winter of 1939.

A study of the worm reveals that it represents a new species of the genus

***Mehratrema polynemusinis*, n.sp.**

(Text-Figs. 1, 2, 3)

Body elongated with anterior end tapering, posterior end broad. Length of the body of the different specimens varies from 1·49 to 1·81 mm. and width from 0·49 to 0·59 mm. being maximum in the posterior half of the body.

TEXT-FIG. 1

Mehratrema polynemusinis n.sp., Ventral view.

C.S., Cirrus sac; *D.*, Ductus ejaculatorius; *e.*, Egg; *Ex.C.*, Arms of excretory vessel; *Ex.P.*, Excretory pore; *G.S.*, Genital sucker; *L.I.C.*, Left intestinal cæcum; *L.T.*, Left testis; *L.T.Vit.D.*, Left transverse vitelline duct; *L.V.*, Left vasa efferens; *L.Vit.*, Left vitellaria; *Met.*, Metraterm; *Oes.*, Oesophagus; *O.S.*, Oral sucker; *Ov.*, Ovary; *Ph.*, Pharynx; *P.Ph.*, Prepharynx; *P.Pr.*, Pars prostatica; *Pr.C.*, Prostrate gland cells; *R.I.C.*, Right intestinal cæcum; *R.T.*, Right testis; *R.T.Vit.D.*, Right trans-vitelline duct; *R.V.*, Right vasa efferens; *R.Vit.*, Right vitellaria; *S.*, Sinus of genital sucker; *S.G.*, Shell gland; *Ut.*, Uterus; *V.*, Vesicula seminalis; *V.S.*, Ventral sucker.

Suckers are nearly equal in size. The oral sucker (*O.S.*) is transversely oval, terminal or subterminal, fairly muscular, measuring 0·16–0·17 × 0·12–0·17 mm. Ventral sucker (*V.S.*) is spherical, slightly post-equatorial,

measuring 0·15–0·19 × 0·14–0·16 mm. It lies at a distance of 0·76–0·97 mm. from the anterior end. It is very feebly muscular.

Oral sucker is followed by a small prepharynx (*P.Ph.*) measuring about 0·02 × 0·02 mm. It communicates posteriorly with a small, muscular, bulbose pharynx (*Ph.*) of 0·04–0·06 × 0·04–0·05 mm. dimensions. Œsophagus (*Oes.*) is elongated, well developed and conical in shape measuring 0·08–0·09 mm. × 0·03–0·04 mm. It bifurcates into two arms at a distance of 0·28–0·29 mm. from the anterior end. The two sinuous intestinal cæca form a sort of base of the two arms of the inverted letter V. They terminate blindly at about 0·04–0·041 mm. anterior to the posterior end of the body. The right arm (*R.I.C.*) is slightly longer than the left (*L.I.C.*), measuring 0·91–1·15 mm. The left measures 0·85–1·0 mm. The posterior end portions of the cæca are crenated.

The two testes are lateral, mostly pre-acetabular and post-ovarian, partly symmetrical or obliquely tandem. They are equatorial, intercæcal and may be, particularly the left, partly supra-acetabular in contracted specimens. The right one (*R.T.*) is slightly elongated and lies just posterior to the ovary, measuring 0·12–0·13 × 0·09–0·11 mm. It is very slightly superposed by the ovary in partially contracted specimens. The left (*L.T.*) is smaller, more spherical and is situated generally slightly posterior to the anterior one. It measures 0·11–0·15 × 0·09–0·10 mm. The two vasa efferentia ducts arise from the inner side of the anterior borders of the testes and meet into a very short, common vas deferens at the right anterior quarter of the ovary; the common duct is almost immediately passing into the vesicula seminalis (*V.S.*) which is a compact pear-shaped supra-ovarian

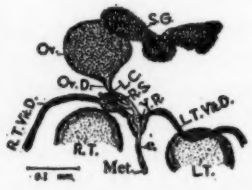
TEXT-FIG. 2

Male end genetalia, Ventral view (Semi-diagrammatic). Lettering as in Fig. 1.

body situated at the base of the cirrus sac, measuring 0·05–0·07 mm. The elongated tubular cirrus sac (*C.S.*) is a tapering curved structure somewhat sickle-shaped, measuring 0·29 × 0·04–0·06 mm. It starts from the anterior right of the ovary, takes a turn to the right, runs alongside the sinus of the genital sucker and opens into the genital sucker (*G.S.*), on the left side of the mid-ventral longitudinal axis of the body. The basal portion, vesicula

seminalis, opens into a tubular pars-prostatica (*P.Pr.*) surrounded by prostrate gland cells. Ductus ejaculatorius (D.) is a muscular elongated tapering organ. The male genitalia opens into a well-developed genital sucker. The genital pore is situated to the left of the mid-longitudinal axis, in between the fork of the intestinal bifurcation and acetabulum and is guarded by a muscular small sucker. It is 0·4–0·41 mm. distant from the anterior end and 0·14–0·24 mm. from the intestinal fork. A characteristic big pear-shaped sinus referred to by Dollfus (1937) as 'genital sinus' with highly muscular walls and deeply staining secretions inside it is a peculiarity of the species. It measures 0·16–0·23 × 0·85–0·21 mm. and is probably confused as a peculiar metraterm.

Ovary (*Ov.*) is spherical, pretesticular and lies slightly in front of the right testis in the anterior half. It measures 0·07–0·12 × 0·09–0·15 mm. In some specimens it touches the anterior border of the right testis. It is superposed by the vesicula seminalis on the right anterior quarter. Shell gland (*S.G.*) is diffuse and lies scattered on the sinus of the genital sucker and part of ovary. The loose mass is somewhat butterfly-shaped. Oviduct



T.XT-FIG. 3

Female genitalia complex, Ventral view (Semi-diagrammatic).

L.C., Laurer's canal; *Ov.D.*, Oviduct; *R.S.*, Receptaculum seminis; *Y.R.*, Yolk reservoir; Other lettering as in Fig. 1.

goes off the Laurer's canal (*L.C.*). A triangular median yolk reservoir lies in between the two testes, slightly anterior to them. The vitellaria (*Vit.*) consist of small spherical follicles, arranged laterally, partly supracæcal, extending from the level of the testes to the end or slightly posterior to the end of intestinal cæca. Vitellaria on two sides are unequal in length. Follicles on the right side start more anteriorly and have slightly a longer extension, measuring 0·67 mm. on the right and 0·50 mm. on the left. The trans-vitelline ducts of the two sides arch over the testes and form a median triangular yolk reservoir. A small though well developed receptaculum seminis (*R.S.*) is present. Uterus (*Ut.*) is post-acetabular and intercæcal. The metraterm (*Mt.*) runs forward by the right side of the acetabulum and in between the two testes, takes a turn to the left alongside the sinus of the genital sucker and opens into the genital sucker on the side of the male genital opening.

Eggs are very minute, numerous, opercular, light yellow in colour and measure 5–8 μ × 2·6–4·1 μ.

The arms of the excretory bladder (*Ex.C.*) take a turn in the anterior region at the level of the œsophagus, run parallel anteriorly and terminate blindly on the oral sucker. The two arms are observed to converge in the region of the testes. The excretory pore (*Ex.P.*) is terminal in the posterior region of the parasite.

Discussion

Dollfus (1937) created a new family *Monodhelminthidæ* and a new genus *Monodhelmis* to accommodate his new species *M. torpedinis* from a Narcacion torpedo. Srivastava (1939) added another new genus *Mehratrema* to the family with his new species *M. dollfusi* as the type species of the genus. He further created two new sub-families, *Monadhelminæ* for the genus *Monodhelmis* and *Mehratreminæ* for the genus *Mehratrema.*

The species described above is assigned to the genus *Mehratrema.* It resembles the other and the only known representative of the genus, *M. dollfusi* recorded from the small intestines of *Scatophagus argus* from India, in the presence of well-developed cirrus sac and genital sucker, almost equal sucker ratio and pre-testicular position of the ovary.

However it differs from it in being a much smaller form and in the absence of the peculiar metraterm, extent of the intestinal cæca and vitellaria, disposition of the uterine coils, position of the testes and genital pore. The intestinal cæca also do not extend posteriorly so far, vitellaria do not extend anteriorly upto ovary; posteriorly the vitellaria do not terminate much anterior to the termination of the intestinal cæca, as in *M. dollfusi.* The shape of the vitellarian follicles is also spherical and not pear-shaped. The disposition of the uterine coils is quite unlike the other species and is confined to post-acetabular region. Relative position of the gonads and acetabulum is also different. The ovary lies on the side of the anterior testis. Genital pore is situated to the left of the mid-longitudinal axis of the body. Genital sucker is smaller, but has well-developed musculature. Acetabulum is very poorly muscular.

Nature of the genital sucker, specially its sinus and structure of the excretory system are interesting.

Peculiar structure of the metraterm of *M. dollfusi* Srivastava, 1939, probably needs further investigation.

HOST	.. *Polynemus indicus, Muræsox talabonoides* and *Sciæna* sp.
LOCATION	.. Intestine.
LOCALITY	.. West Indian Coast, Bombay.

In conclusion, I am highly grateful to Dr. M. A. Moghe, Head of the Department of Zoology, for his keen interest and help to me. I also wish to thank Dr. S. M. Lele of the Elphinstone College, Bombay.

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VOLUME RELATIONS OF THE NUCLEUS IN APODAN SPERMATELEOSIS

By B. R. Seshachar

(Department of Zoology, Central College, Bangalore)

Received April 20, 1943

(Communicated by Prof. A. Subba Rau)

It is well known that one of the most important changes in spermateleosis that relate to the nucleus is its condensation. The nucleus of the early spermatid and that of the fully formed spermatozoon are often very different in size, shape and form, and while the former is generally spherical, the latter exhibits great variety of form in animals. In fact it is one of the obvious facts in animal cytology that the nucleus is amongst the most variable factors in the spermatozoon. Even closely related animals display this diversity in the form and size of the nucleus. However fantastic in shape and variable in size, the nucleus of the adult spermatozoon arises from a transformation of the original spherical nucleus of the spermatid.

All accounts of spermateleosis in animals relate mainly to the changes that takes place in the cytoplasmic bodies,—the mitochondria, the Golgi bodies and the centrosome. Very few of them deal with the nucleus. I know of no work that deals with the size and volume relationships of the nucleus in the different stages of spermateleosis. Literature does not show any references to a study of the relationships between the spermatid nucleus and the nucleus of the spermatozoon. In fact, in the majority of cases, the establishment of any relationship between the two appears impossible because of the weird shapes the nucleus of the sperm takes in its final form. Apart therefore from the observation that generally in animals the main change that takes place in the spermatid nucleus in its transformation into the nucleus of the adult sperm is one of consolidation and condensation, no other facts are available. Nothing is known of the extent of this condensation or the change of volume involved in the process. That the condensation implies also a reduction in nuclear volume, it has been inferred; for, it is well known that the nucleus of the adult sperm is a solid mass of chromatin, while that of the early spermatid like the resting animal nucleus, contains, in addition to the chromatin, other material comprehensively called the " nuclear sap ". The process of condensation must therefore consist of a casting off of this extra material and if it were possible to determine the relative volume relationships of the nucleus

in different stages of spermateleosis, and especially at the beginning and at the finish of the process, an idea of the extent of this condensation might be obtained. But this is a matter of great difficulty; for, while it is quite possible to determine the volume of the spherical spermatid nucleus, it is a matter of great difficulty, and in some cases, of impossibility, to estimate the volume of the irregular and fanciful sperm nucleus. That appears to be the reason for the lack of our knowledge of the volume relationships of the nucleus in the spermatid and the spermatozoon.

In my study of the spermateleosis of *Ichthyophis glutinosus* (Amphibia: Apoda),* it was observed that amongst the changes involving the nucleus during spermateleosis was a reduction in its size and change in its form. The nucleus of the early spermatid is spherical but as soon as spermateleosis starts, the nucleus elongates and this elongation continues till a maximum is reached. After this a shrinkage and condensation of the nucleus result in the compact cylindrical rod which is the nucleus of the fully formed sperm. An examination of other genera of Apoda in my possession shows that the changes in the nucleus described for *Ichthyophis* occur in them also, the spermatid nucleus undergoing first a process of elongation and then one of contraction and consolidation resulting in the nucleus of the adult sperm. It then struck me that it would probably be of interest to determine the changes in volume the spermatid nucleus passes through during its transformation into that of the spermatozoon in the different genera of Apoda in my possession. In this respect the apodan material happens to be particularly favourable; for, in all stages of spermateleosis, the form of the nucleus of the transforming spermatid is such that its volume can be determined by mathematical formulæ. This is not so in many other animals where the final form of the nucleus of the fully formed spermatozoon and also that of the intermediate stages are such that the nuclear volume cannot be easily determined by mathematical formulæ. The lance-shaped head of the urodele sperm, the spirally twisted head of that of the bird, the spoon-shaped and flattened head of the sperms of many mammals do not lend themselves for an easy determination of the volumes of their nuclei. It is only in the Apoda that this determination is possible and in this connection I have examined the following five species:

Ichthyophis glutinosus Linn.
Uræotyphlus narayani Seshachar
Dermophis gregorii Blgr.
Siphonops annulatus Mikan
Gegenophis carnosus Bedd.

In the matter of the determination of the nuclear volumes, the following procedure was adopted. In each species three stages were selected for measurements:

* In press.

Stage I. Nucleus of the early spermatid.
Stage II. Nucleus at its greatest or maximum elongation.
Stage III. Nucleus of the fully formed sperm.

The first stage is a sphere while stages II and III are cylinders. Twenty counts of the measurements of each of these stages in each species were made and the average of these twenty was taken for the calculation of the nuclear volumes of the stages. The volumes in the three stages are given below (Table I) and the same table is shown grapically in Fig. 1.

TABLE I

Nuclear volume in cubic microns

Species	Earliest spermatid	Spermatid at maximum elongation	Fully formed sperm
Ichthyophis glutinosus	267·9	179·2	25·1
Uraeotyphlus narayani	164·7	77·8	17·1
Dermophis gregorii	113·1	73·3	23·3
Siphonops annulatus	408·0	189·3	22·9
Gegenophis carnosus	209·4	81·7	22·6

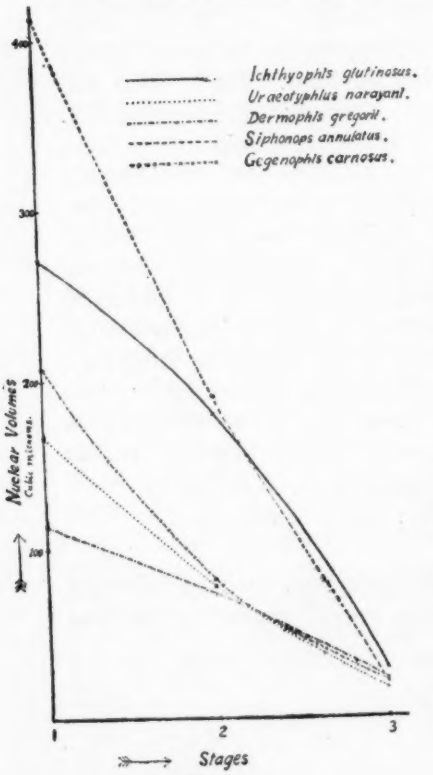

FIG. 1

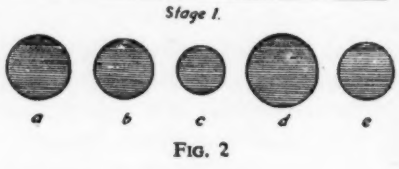

FIG. 2

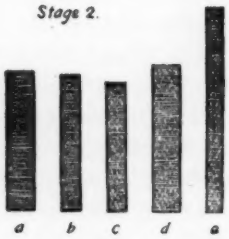

FIG. 3

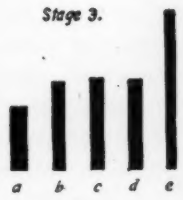

FIG. 4

FIG. 1. Graph to show the fall in nuclear volume during spermateleosis in the five species of Apoda (see also Table I).

FIGS. 2, 3 and 4. Figures to show the relative sizes of the nuclei in the three different stages of spermateleosis. × 1150.

(*a*) *Ichthyophis glutinosus*; (*b*) *Uraeotyphlus narayani*; (*c*) *Dermophis gregorii*; (*d*) *Siphonops annulatus*; (*e*) *Gegenophis carnosus*; Fig. 2. Early spermatid; Fig. 3. Transforming spermatid at its greatest elongation; Fig. 4. Fully formed sperm.

Figs. 2, 3 and 4 give a comparative idea of the nucleus in the three stages. Fig. 2 shows the size of the early spermatid nucleus in the five species, Fig. 3 that of the nucleus in its maximum elongation, and Fig. 4 is the nucleus of the fully formed spermatozoon. The magnification is the same in all cases, *i.e.*, 1150 diameters.

It would perhaps be useful to visualise the change as well as the ratio of the nuclear volumes as between the three stages and I append below the following two tables.

TABLE II

Change in nuclear volume from stage to stage

Species	I–II	II–III	I–III
Ichthyophis glutinosus	88·7	154·1	242·8
Uraeotyphlus narayani	86·9	60·7	147·6
Dermophis gregorii	39·8	50·0	89·8
Siphonops annulatus	218·7	166·4	385·1
Gegenophis carnosus	127·7	59·1	186·8

Note.—I–II indicates the diminution in nuclear volume in passing from Stage I to Stage II ; II–III indicates the diminution in passing from Stage II to Stage III. The third column is the sum of the first two.

TABLE III

Ratio of nuclear volumes in the three stages

Species	II/I	III/II	III/I
Ichthyophis glutinosus	0·67	0·14	0·09
Uraeotyphlus narayani	0·47	0·22	0·10
Dermophis gregorii	0·65	0·32	0·21
Siphonops annulatus	0·46	0·12	0·06
Gegenophis carnosus	0·39	0·28	0·11

Note.—II/I indicates the ratio of the volumes in the second and the first stage ; III/II indicates the ratio in the third and the second stage. The third column is the product of the first two.

Conclusions

Seeing that this is the first attempt at a determination of the changes in the volume of the nucleus during spermateleosis, it would be hazardous to draw any far-reaching conclusions on the data available. But one striking fact that emerges from a study of the above figures is the

enormous reduction in the volume of the nucleus from the spermatid to the fully formed sperm. This reduction is approximately 95% in *Siphonops annulatus*, 90% in *Ichthyophis glutinosus*, *Uræotyphlus narayani* and *Gegenophis carnosus* and 80% in *Dermophis gregorii*. It is therefore clear that the chromatin of the nucleus accounts only for a small quantity of its volume.

Another fact that strikes one from an examination of the Graph (Fig. 1) and Table I is that so far as the five species of Apoda are concerned, in spite of the large variation in the nuclear volumes of the different species in stages I and II, the volume in the third stage, *i.e.*, in the fully formed sperm, is nearly the same in all the species. What significance is to be attached to this fact will not be clear till more species are examined, but the close similarity in nuclear volume of the adult sperms of these five different species of Apoda is interesting.

SURFACE AND INTERIOR EFFECTS IN UNSTRIATED MUSCLE PRODUCED BY VARIOUS IONS

By Inderjit Singh

(From the Physiological Laboratory, Cambridge)

Received March 5, 1943

(Communicated by Prof. B. K. Singh, sc.d., d.sc., f.a.sc.)

Tonic contractions produced by various ions in unstriated muscle are diminished by two agencies, calcium and increase in osmotic pressure of the medium.[1,2] It is reasonable to assume that calcium produces a surface effect, and increase in osmotic pressure of the medium produces an interior effect by increasing the concentration of ions inside the muscle fibres[3]; increase in osmotic pressure of the medium does increase the concentration of ions within the fibres.[4,5] When potassium is applied to the surface of amœba, the viscosity of protoplasm is increased, while if it is injected into the interior, then the viscosity is decreased.[6] It is interesting to note, that in unstriated muscle, when potassium is applied to the exterior, the viscosity is increased,[7] while if the concentration of potassium is increased within the fibres, the viscosity is decreased;[8] the effects of potassium on the amœba and unstriated muscle appear to be very similar. Acids produce a double effect on Paramœcia, first a rapid surface action causing excitation, secondly a slowly developing inhibition produced by the acid penetrating the cell.[9] Weaker acids produce their effects by penetrating into the cells.[10] Amonium produces effects by surface action, as well as by penetrating into the cells.[11,12]

It is reasonable to assume that ions which are known to penetrate cells, may produce their action not only on the surface, but also in the interior of the cells. Excitation in unstriated muscle appears to be produced by difference in concentration of ions within and without the fibres, and it would be expected that the contraction produced by ions which are known to penetrate the muscle fibres less rapidly, would be diminished by those ions which are known to penetrate rapidly. Ammonium and potassium are known to penetrate cells rapidly, while the sodium salts, such as chloride, are known to penetrate less rapidly. In this paper are described action of ions on unstriated muscle which are known to penetrate the fibres, and of those which are known to penetrate with difficulty only.

The action of ions has been studied by recording stretch curves of *Mytilus* muscle.[1,13,14]

Results

Effect of potassium.—In 6 experiments 0·1 M KCl produced a contraction which took over 12 hours to subside (Fig. 1). The slow subsidence suggests diffusion of ptoassium into the fibres; this view is supported by the fact that with larger concentrations, upto 0·5 M KCl, the contraction subsides sooner. With 0·5 M KCl it subsides in a few minutes.

In the absence of calcium, the contraction produced by 0·1 M KCl subsides in a few minutes (6 experiments). In the absence of calcium, potassium penetrates the fibres more rapidly.[4,5]

In 3 experiments, potassium (0·3 M KCl) neutralised the contraction produced by 0·07 M $BaCl_2$ in 15 minutes (Fig. 2).

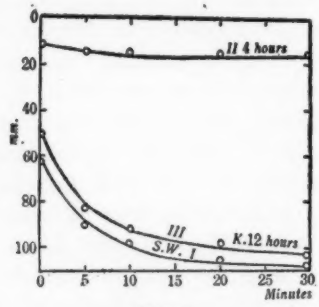

FIG. 1

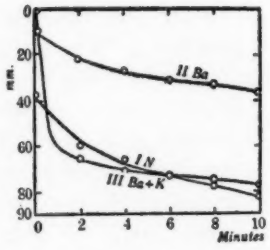

FIG. 2

FIG. 1. *Mytilus* muscle. Stretch curves. 1st curve in *Mytilus* saline; 2nd curve in 0·1 M KCl after 4 hours immersion; and 3rd curve after 12 hours immersion. FIG. 2. *Mytilus* muscle. Stretch curves. 1st curve in *Mytilus* saline; 2nd curve in 0·07 M $BaCl_2$; and 3rd curve in 0·07 M $BaCl_2$+0·4 M KCl.

Effect of ammonium.—Ammonium is known to penetrate cells rapidly and 0·1 M NH_4Cl neutralised the contraction produced by 0·1 M KCl in 6 experiments, that produced by 0·07 M $BaCl_2$ in 3 experiments, that produced by 0·5 M NaCl in 3 experiments.

Effect of sodium.—In isotonic solution of sodium chloride, unstriated muscle gains sodium,[4,5] and the contraction produced by sodium chloride slowly subsides (4 experiments); 0·1 M KCl completely neutralises the contraction produced by sodium chloride (Fig. 3).

Effect of hydrogen ions.—Hydrogen ions are most rapidly moving ions and they neutralise the contraction produced by all substances. Change of pH from 7·8 to 5 neutralised the contraction produced by 0·1 M KCl in 6 experiments (Fig. 4) that produced by adrenaline (1 in 10^5) in 4 experiments, that produced by acetylcholine (1 in 10^6) in 4 experiments, that produced by

veratrine (1 in 1,000) in 6 experiments, that produced by caffeine (1 in 1,000) in 3 experiments.

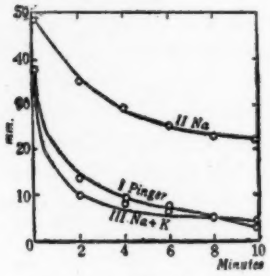

FIG. 3

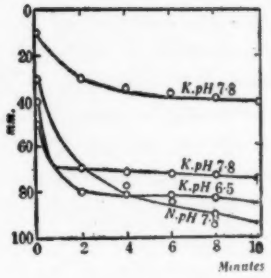

FIG. 4

FIG. 3. *Mytilus* muscle. Stretch curves. 1st curve in *Mytilus* saline; 2nd curve in 0·5 M NaCl; and 3rd curve in 0·1 M KCl + 0·4 M NaCl. FIG. 4. *Mytilus* muscle. Stretch curves. Effect of pH on the potassium contraction N = normal; K = 0·1 M KCl.

Effect of glucose and urea.—Isotonic solution of glucosa produces contracture in unstriated muscle. In 6 experiments addition of 5 grams of urea to 100 c.c. of isotonic solution of glucose neutralised the contracture completely (Fig. 5). Glucose does not penetrate the muscle fibres,[15] while urea does so.[15,16] The glucose contracture is also neutralised by potassium, and ammonium.

Effect of withdrawal of urea and hydrogen ions.—A muscle treated with excess of urea in *Mytilus* saline, developes much tone when the urea is withdrawn (6 experiments). Withdrawal of hydrogen ions produces a similar effect (3 experiments, Fig. 6). This may be due to difference in concentration of ions inside and outside the fibres.

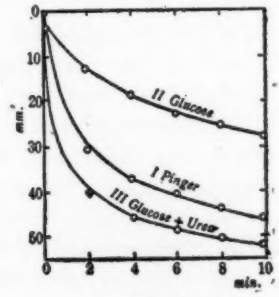

FIG. 5

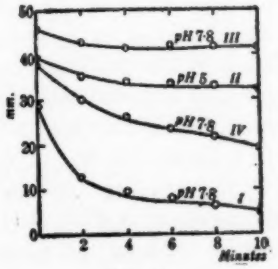

FIG. 6

Fig. 5. *Mytilus* muscle. Stretch curves. 1st curve in saline; 2nd curve in glucose; and 3rd curve in glucose + urea. FIG. 6. *Mytilus* muscle. Stretch curves.

Effect of osmotic pressure.—If the saline is made hypertonic by addition of sodium chloride, the concentration of ions within will increase. As sodium chloride does not readily penetrate the cells, the first effect should be to increase the excitability to potassium, and decrease that to A.C., as soduim chloride would potentiate the response to potassium and antagonise that to A.C., because contracture producing substances have such an effect. This was found in 6 experiments. As the concentration of potassium within the fibres rises owing to abstraction of water, an opposite effect is produced subsequently. Hypotonic solutions produce opposite effects.

The effect of nicotine (1 in 1,000).—In 3 experiments it neutralised the contraction produced by acetylcholine (1 in 10^5) at pH 7·8; at pH 6 it had no appreciable or slight effect.[18] This is probably due to the fact, that nicotine penetrates more rapidly in alkaline solutions as undisassociated base; ammonia penetrates more rapidly in alkaline solutions as undisassociated hydroxide.[19]

Discussion

It appears that substances, as they enter the unstriated muscle fibres, produce inhibition of tone. In the presence of eserine acetylcholine produces inhibition whilst in the absence of eserine it produces excitation of the superior cervical ganglion. If acetylcholine is destroyed as it enters the cells, then excitation would result, because difference in concentration within and without the fibres would be maintained, but if it is prevented from being destroyed, then inhibition would result, as the difference would not then be maintained. Similarly the occurrence of contrraction with small doses and inhibition with larger doses, such as those of histamine[20] and plasmoquin[21] acting on the guinea pig uterus, can be explained as follows: with small concentrations these drugs might not penetrate the cells, but with large concentrations they might do so.

The occurrence of Wednesky inhibition might also be explained in the same way. Cowan has found that when the nerve to a frog's sartorius was stimulated, Wedensky inhibition at the nerve ending soon developed, but this inhibition occurred earlier and was deeper in the presence of prostigmine. If acetylcholine is liberated from the nerve endings, then inhibition would result if it enters the fibres. If the liberation was excessive, or if it was protected by eserine, then inhibition might result, in the first instance, owing to the fact that the rate of destruction of the transmitter does not keep pace with its entrance and in the second instance, the destruction of acetylcholine is prevented by eserine. With potassium also in *Mytilus* muscle, the tension subsides quicker with larger concentrations (0·2–0·5 M KCl) than with smaller concentrations (0·1 M KCl).

The above experiments suggest that excitation is produced when a certain difference in concentration of ions is produced within and without. If potassium is added slowly to *Mytilus* muscle, then no stimulation might result. This is due (1) either to diffusion of ions into the fibres as fast as their concentration is rasied or, (2) to adaptation. Adaptation certainly occurs. If calcium is excluded, then the muscle becomes inexcitable to A.C., potassium or adrenaline; the latter two produce relaxation only. It may be assumed, that permeability is so much increased by the lack of calcium that diffusion of potassium and adrenaline into the muscle is rapid. The effect of calcium lack might be ascribed as due to changes in adapatation; but calcium lack would diminish adaptation and this would produce an effect opposite to that described above, *viz.*, increase the excitability to adrenaline and potassium. So the changes do not appear to be due to changes in adaptation.

When potassium is added to the muscle, the surface fibres should contract immediately, and the rest of the fibres as potassium diffuses into the interspaces. But it is often found that the maximum tension is reached in a minute or two and the muscle begins to relax. It is thus evident that the potassium reaches the inner fibres too slowly to cause excitation. If accommodation is diminished, such as with cyanide, then the muscle continues to contract for half an hour or more (Fig. 7). This view is supported by the fact

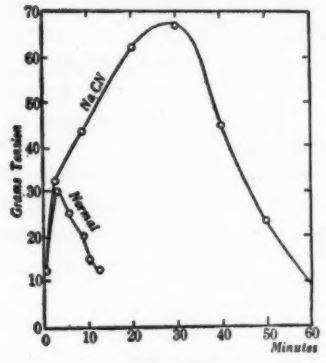

FIG. 7

Mytilus muscle. Contraction produced by 0·1 M KCl.

that in barium to which accommodation is slow, the tension rises slowly. Normally, the responses recorded with potassium are those of the surface fibres; such an inference is justified as the responses are quite regular.

Summary

Ions such as potassium, ammonium, hydrogen, to which the mu scleis permeable, neutralise the contractures produced by ions to which the muscle is comparatively less permeable, such as sodium chloride, adrenaline, acetylcholine. This suggests that excitation is caused by difference in concentrations of ions within and without the cells.

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REVERSAL EFFECTS IN UNSTRIATED MUSCLE

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(Communicated by Prof. B. K. Singh, sc.d., d.sc., f.a.sc.)

Inhibitory reflexes are converted into excitatory ones by strychnine (Sherrington, 1905, 1906; Gasser, 1908; Seeman, 1910; Sherrington and Owen, 1911; Moore, 1919; Knowlton and Moore, 1917; Cushny, 1919). Chloroform has the opposite effect (Gasser, 1908; Mathison, 1912; Sherrington and Sowton, 1911). Ether reverses the effect of histamine (Heilbrunn, 1937). Reversal without the influence of drugs is described by Magnus (1909). Nicotine reverses the effect of the vagus (Dale, Laidlaw and Symons, 1910). Cysticine stops the secretion caused by the stimulation of the chorda tympani (Dale and Laidlaw, 1911). After Curare, the normal contraction of the bladder produced by stimulation of the sacral nerve is followed by inhibition (Langley, 1911). Ergotoxin converts the normal vaso-constrictor effect of the abdominal sympathetic on the hind leg into a vasodilator one (Dale, 1906). Ergotoxin reverses the effect of adrenaline on the melanophores of Fundulus (Spaeth and Barbour, 1917). Pearce found that the vaso-constrictor effect of adrenaline is converted into vaso-dilator one by the absence of calcium.

The experiments described in this paper have been performed on *Mytilus* muscle, frog stomach, dog stomach, dogretractor penis and guinea pig uterus (Singh, 1936, 1937, 1938 *a*, *b*, *c*, *d*, *e*, *f*; 1939 *a*, *b*; 1940; 1942 *a*, *b*; 1943 *a*, *b*, *c*, *d*, *e*; Rao and Singh, 1940; Gokhale and Singh). Some of the effects have been studied by recording stretch curves.

Results

Reversal effects are brought about by (1) hydrogen ions; (2) calcium ions; (3) sodium chloride; (4) drugs; (5) physiological conditions such as tone, adaptation, fatigue and inexcitability; (6) change of initial length.

Effect of hydrogen ions.—A change of reaction from alkaline to acid reverses the effect of most substances. The most important effect of hydrogen ions is to diminish or convert excitatory effect into an inhibitory one. Thus in *Mytilus* muscle, drugs such as adrenaline (6 experiments), veratrine

(6 experiments), eserine (2 experiments), caffeine (6 experiments), produce contraction in alkaline and inhibition in acid solutions. In frog stomach, the excitability to alternating current and potassium is reversed by change of reaction, if the osmotic pressure of the saline is increased to 1·3 times normal by adding sodium chloride (6 experiments). In guinea pig uterus excitatory action of calcium is converted into an inhibitory one (6 experiments): if the effect is inhibitory, hydrogen ions increase the inhibitory action (Fig. 1).

Effect of calcium ions.—In the absence of calcium, adrenaline (6 experiments) and potassium (6 experiments) produced inhibition (Fig. 2), though the immediate effect is in the opposite direction; alternating current also may produce inhibition instead of contraction. In summer *Mytilus* muscles, most substances produce inhibition. These muscles when immersed in saline, lose weight, indicating the presence of excess of calcium, as the latter causes the muscle to lose weight (Singh, 1938 *b*).

It is interesting to note that ions that produce inhibition, cause the muscle to lose weight. Thus calcium and hydrogen ions in *Mytilus* muscle, sodium chloride in frog muscle, small concentrations of potassium and magnesium in *Mytilus* muscle produce inhibition as well as loss of weight.

Effect of adaptation.—After adaptation, an excitatory effect may be converted into an inhibitory one. In this connexion, the mutual antagonistic effects of calcium on the one hand and potassium, ammonium and magnesium on the other hand in the frog stomach is intersting. Fig. 3 shows

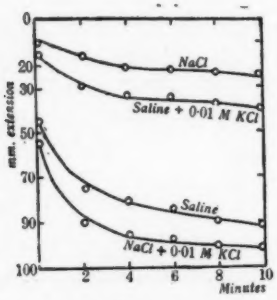

FIG. 2

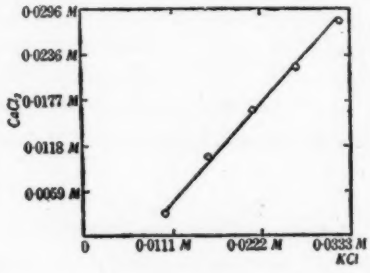

FIG. 3

the concentrations of calcium and potassium which have such action. Singly these concentrations of calcium and potassium are excitatory and depress the excitability to alternating current but together they have an opposite action. This suggests that if calcium be liberated, the effect of potassium will be

reversed after adaptation. Calcium is liberated in protoplasm under a variety of conditions (Heilbrunn, 1937).

Effect of fatigue.—As adaptation with continous stimulation, and fatigue with intermittent stimulation are identical (Singh, 1938 *d, f*; 1939 *b*), the latter may produce a reversal effect. This is best seen in the giunea pig uterus, if it is frequently stimulated with potassium. The excitatory effect is completely reversed (Fig 4; 6 experiments). This is probably due to liberation of calcium.

Effect of inexcitability.—If *Mytilus* muscle is inexcitable to adrenaline, eserine, acetylcholine, caffeine, veratrine, these drugs produce inhibition. If *Mytilus* muscle or frog stomach is rendered inexcitable to alternating current by excess of potassium or anions such as bromide, iodide, nitrate, caffeine, adrenaline, acetylcholine, veratrine, etc., only inhibition is produced as a result of the passage of the current.

Effect of tone.—M'Crea, M'Swiney and Stopford, Veach (1925) found that stimulation of the vagus caused contraction of relaxed stomach, and relaxation of contracted stomach. Increase of tone may reverse an excitatory effect. In the guinea pig uterus, which shows excess tone, most substances which produce contraction in other unstriated muscle, produce inhibition (Singh, 1942 *b*).

Effect of initial length.—This is best seen in the guinea pig uterus. If alternating current produces inhibition, then by increasing the length of the muscle, this effect is completely reversed (6 experiments).

Effect of sodium chloride.—In *Mytilus* muscle, in the absence of sodium chloride in isotonic glucose a contracture develops; small concentrations of potassium (0·01 M KCl) which cause inibition in the presence of sidium chloride, now cause further contraction and larger concentrations (0·1 M KCl), that usually cause contraction, produce inhibition.

The guinea pig uterus shows the reversal effect produced by change in the concentration of sodium chloride very well (8 experiments; Fig. 5). In small concentrations of sodium chloride, calcium and potassium produce contraction instead of inhibition.

Effect of cations, anions and drugs.—In the guinea pig uterus cations reverse the inhibitory effect of alternating current, while anions produce an opposite action. In *Mytilus* muscle anions reverse the excitatory effect of alternating current, while the cations produce an opposite effect.

Caffeine (saturated solution in *Mytilus* saline) in summer *Mytilus* muscles, which are inexcitable to potassium converts the depressor effect

of adrenaline (6 experiments) and veratrine (6 experiments) on the response to alternating current into a potentiating one; it also converts the inhibitory effect of adrenaline into a stimulatory one; calcium produces similar effects.

In *Mytilus* muscle anions (Br, I, NO_3, SCN, CN) and drugs such as strychnine, ephedrine, veratrine, adrenaline, acetylcholine potentiate the response to potassium (0·1 M KCl) and may convert its inhibitory effect into an excitatory one.

Discussion

The reversal effect produced by hydrogen ions suggest a change in the sign of the muscle membrane. It is also possible that the colloidal properties of the muscle membrane alter with the hydrogen-ion concentartion. It has been shown (Singh, 1938 *b*; 1939 *b*; 1942 *b*), that the physiological effects of various ions varies in the same order in which they act on the muscle colloids. Hydrogen ions reverse the effect of the above ions on colloids. Thus the cations $Li < Na < K < NH_4$ favour precipitation of positively charged (*i.e.*, acidified) protein in the order shown; in alkaline solutions the order is reversed. Calcium probably alters the colloidal constitution of the muscle membrane.

It is well known that inanimate membranes are often selectively permeable to ions, in that they offer more resistance to anions than to cations and *vice versa*. Indeed, inanimate membranes have been prepared which are completely impermeable either to anion or to cation. This impermeability to one species of ion or another seems to depend on the sign of the electric charge on the pores of the membrane. It is very probable that living membrances may show a differential permeability towards anions and cations.

Such a differential permeability appears to explain the action of drugs which are known to be effective in very minute concentrations. Thus in *Mytilus* muscle the action of sodium chloride is excitatory, and adrenaline produces contraction; in frog muscle it is inhibitory and adrenaline produces inhibition. In dog stomach the action of sodium chloride as well as that of adrenaline may be either excitatory or inhibitory. It thus appears that adrenaline sensitises the muscle to ions without. Now it has been shown (Singh, 1942 *b*) that the action of sodium is antagonistic to that of chloride, the effect of the former being inhibitory and the latter excitatory, the net effect of sodium chloride depending upon as to which of these ions predominates. The predominance of one ion or the other might depend upon the charge of the membrane, and this would explain the reversal effect produced by hydrogen ions.

It is also possible that the cations just reinforce each other, and if there is a delicate balance between the actions of sodium and chloride, this balance might be upset by increase in the cation concentration when the reaction is changed from alkaline to acid, and by liberation of calcium. Hydrogen and calcium ions would then convert an excitatory effect into an inhibitory effect, and so also those conditions in which calcium is probably liberated, such as adaptation and fatigue.

There is a relation between excitability and the nature of the response. Ordinarily a subliminal stimulus causes relaxation, and a liminal or supraliminal, contraction. If the excitability is decreased by ions, drugs or tone or is naturally low, then greater strength of the stimulus is necessary to produce contraction; otherwise inhibition is the result. This can be explained if it is assumed that a stimulus is composed of an excitatory and an inhibitory factor. If the first is rendered ineffective, then the second produces inhibition . Fatigue abolishes the excitatory factor, without affecting the inhibitory factor, and thus produces a reversal effect.

If the muscle contracts on stimulation, then it is obvious that the excitatory factor predominates. If the muscle is already contracted, then the inhibitory factor only acts, so that some agencies cause a relaxed muscle to contract and a contracted muscle to relax.

Summary

(1) Hydrogen ions may convert an excitatory effect into an inhibitory one.

(2) Calcium, sodium chloride and caffeine may produce reversal effects.

(3) Presence of tone alters an excitatory effect into an inhibitory one.

(4) Anions may convert an inhibitory effect into an excitatory one, and cations may produce an opposite effect.

(5) Reversal effects are also produced by adaptation, fatigue, inexcitability and change of length.

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EXPLANATION OF FIGURES

Fig. 1. Guinea pig uterus. (*a*) Excitatory effect of calcium at pH 8. The muscle is previously immersed in postasium-free saline. Potassium is added at (1). Calcium withdrawn at (2). Potassium is withdrawn at (3) and added at (4). Calcium is added at (5) and potassium is withdrawn at (6). *Note* calcium reverses the action of potassium. Potassium is added at (7). *Note* calcium increases the primary inhibition, as well as the subsequent adaptation. (*b*) At pH 6·5 same as (*a*). Potassium is added at (1). Calcium is withdrawn at (2). Potassium is withdrawn at (3) and potassium added at (4), calcium added at (5). (*c*) Muscle previously in potassium-free saline, at pH 6·5 potassium added at (1), withdrawn at (2). pH changed to 7 at (3) and potassium added at (4), withdrawn at (5). (*d*) Same muscle in pH 8 in potassium-free saline. Potassium is added at (1) ,withdrawn at (2) ; pH changed to 6 at (3) and potassium added at (4). Note that hydrogen ions increase the inhibition as well as the subsequent adaptation.

Fig. 2. *Mytilus* muscle. Effect of potassium in the presence and absence of calcium.

Fig. 3. Frog stomach. Concentrations of potassium and calcium which have mutually inhibitory effect.

Fig. 4. Guinea pig uterus. Repeated stimulation with 0·13 M KCl ; excitation (1st figure) passes into inhibition (2nd figure).

Fig. 5. Guinea pig uterus. Muscle in mammalian saline pH 8. Potassium withdrawn at (1) and added at (2). At (3) sodium chloride reduced to 80 p.c. of normal. Potassium withdrawn at (4), and added near the end. Potassium withdrawn at (5) in sodium chloride 60 p.c. of normal and added at (6). Potassium added at (7) and (9) in sodium chloride 20 p.c. of normal, and withdrawn at (8). Note the disappearance of tone in 20 p.c. sodium chloride and reversal of the effect of potassium in sodium chloride 20–80 p.c. of normal concentration.

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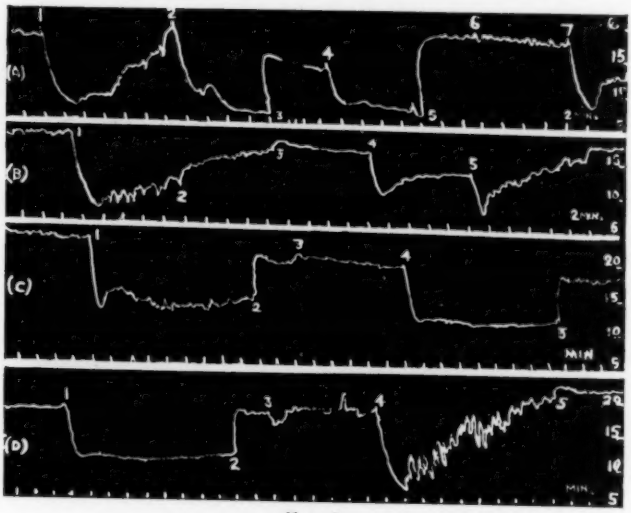
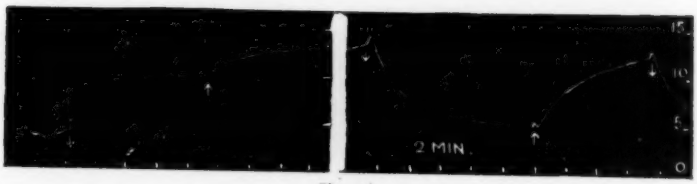


FIG. 1



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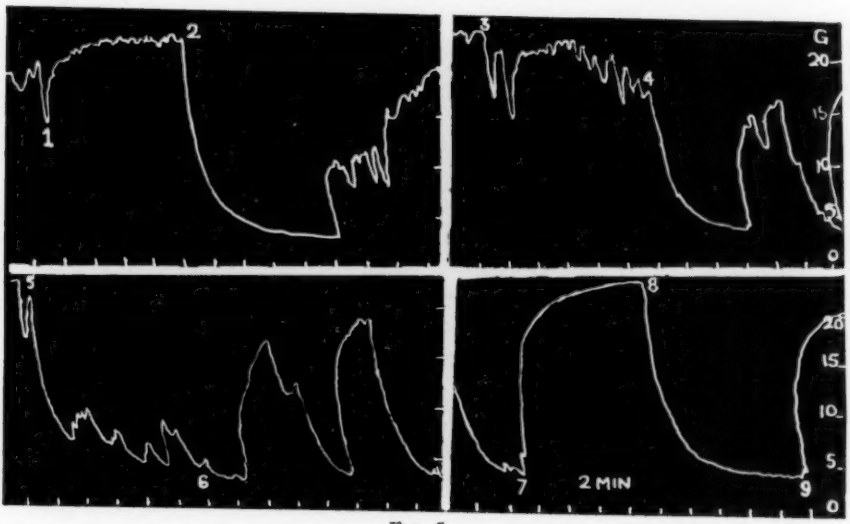

FIG. 5

ON THE STRATIGRAPHIC AND TECTONIC CORRELATIONS OF THE SIRMOOR ROCK FORMATIONS, SIMLA HIMALAYAS

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Received May 14, 1943
(Communicated by Prof. L. Rama Rao, F.A.Sc.)

In a recent paper on "Some Tectonic Observations in the Sirmoor Himalayas" which was read at the Baroda Session of the Indian Science Congress, the author had recorded some field observations within the confines of the Sirmoor State, Simla Hills, which have led him to some new interpretations as to the nature of certain rock types and their stratigraphic position. The paper evoked some discussion both in the sectional meeting of Geology and later through correspondence from geologisst who are most familiar with the region under study and it was thought proper to include in the body of the paper some new arguments and observations which have a direct bearing on the issues raised.

The Sirmoor Hills form a part of the Simla Himalayas and exhibit a close similarity both in lithology and build with the Simla Hills on the north-west and show a great affinity with the Garhwal Hills to the east. It is possible that being situated in the bend of the Himalayas where the strike is gradually changing from a dominant N N W—S S E direction of the Simla Hills to W N W—E S E direction of the Garhwal Hills, the structure includes elements of both in a possibly more complex form.

The Sirmoor Hills have been the subject of study by the officers of the Geological Survey of India since the sixties of the last century, when Medlicott, Oldham and Middlemiss, the doyens of Indian Geology, laid the foundation of our geological knowledge of the Himalayas. The basic ideas of the rock types of the various formations and their probable correlations were already established in the last century. But the present day conceptions of the tectonic build of the Himalayas date only from 1928, when Pilgrim and West published their Memoir on the structure and correlation of the Simla Rocks.[1] They have applied the modern ideas on the tectonic structure of mountains, as originally developed in the Alpine study in Europe since the nineties of the last century, and have recognised a number of Nappes or Low-angle-overthrusts in the Simla region. This recognition also led to the revision of stratigraphic classification of the rock types and thus to put the geological history of the unfossiliferous outer part of the

Himalayas on surer footing. It took over one full generation to recognise the Alpine structures in the Himalayas. This is, of course, not to be wondered at since the Himalayas have been much too inhospitable and many parts inaccessible. Moreover the economic bias of the Geological Survey of India did not encourage the exploration of large tracts of the Himalayas obviously poor in essential mineral resources.

The Simla Himalayas appear to a certain extent exceptional in receiving a great deal of attention from the Survey and the detailed studies of Pilgrim, West and later those of Auden have opened out new vistas in the study of these parts. During a short study of the hills composing the Sirmoor Himalayas for the purpose of investigation of economic minerals of the State in the summer of 1941 the author had an opportunity of observing the various geological formations, their lithological characters and tectonic relationships. During the field work he had for his guidance the excellent maps of the Simla Hills by Pilgrim and West and of the Krol Belt by Auden. Owing, however, to the short time at his disposal detailed investigations could not be made. The views, here expressed, therefore, have no claim to finality such as is possible only after intensive field study. It is therefore intended to present these observations for the consideration of the future worker so that he may bring about a better understanding of the tectonics of these hills.

Blaini Boulder Bed

The first observation to be made in this connection is regarding the nature of the " Blaini Boulder Bed ". In the studies of the various regions of the Himalayas the Blaini Boulder Bed has nearly always been taken as the datum horizon in order to assign stratigraphical positions to the associated unfossiliferous rock formations. This boulder formation is known to occur almost continuously from Hazara and Salt Range on the north-west through Kashmir, Punjab Himalayas, Spiti and Simla to Garhwal Himalayas in the east and for nearly all of these occurrences the Permian glaciation is supposed to be the agent of deposition. The associated underlying beds are therefore given the Lower or Middle Palæozoic age while the overlying rocks are regarded as Permo-Triassic in age. In several cases the degree of metamorphism of the associated rocks has been altogether disregarded in deciding the age. Thus, certain quartzites in most respects comparable to Jaunsar or Jutogh quartzites have been assigned a Jurassic age because they appear to lie conformably over the " Blaini-Krol succession of Carbo-Triassic age ".

In another communication the author has shown that much of what goes under the name of Blaini boulder bed appears more likely to be a thrust

breccia or a tectonic conglomerate folded in by later phases of the same orogenic movement of middle Tertiary period, and further that it does not possess that stratigraphic importance which has been attributed to it nor does it prove the existence and extension of glaciers which were supposed to have covered a large part of the Gondwana continent during Permo-Carboniferous times.

Nummulitics of the Tons

An extensive outcrop of Nummulitic Limestone was observed along the Tons river east of Chandpur. The outcrop was traced nearly continually from Sayasu (Kwanu) to Senj and in all likelihood the same continues much further north. This limestone is hard, compact and highly fossiliferous being full of Nummulites. This outcrop has not been marked in the map by Pilgrim and West and only a very small spot near Sayasu has been marked by Auden as " Probably Nummulitic " in his map of the Krol Belt. Later Auden appears to have noted this Nummulitic formation east of the Tons as he has shown it in his Tectonic Sketch Map of the Garhwal Himalayas.

On the Sirmoor side of the Tons the outcrop of the Nummulitic limestone is comparatively small but by no means insignificant. It is always in contact with the dark compact slates which are dipping at high angles and show a distinct tectonic junction.

The main outcrop of the Nummulitics is to the east of the river where it occurs over a large area forming high hills. In the Simla region the Nummulitic limestone generally forms a very minor part of the Subathu formation in which the variegated splintery gypseous shales predominate. On the other hand in the Tons outcrop of these Subathus the nummulitic limestone appears to form the bulk of the formation almost to the exclusion of the shaly facies.

This outcrop, associated as it is with Simla Slates, appears in all probability to be autochthonous, a feature already recognised by Auden.[2]

The Mandhalis of the Shillai Syncline

Auden has mapped the whole region between the Tons R. and Juini Dhar as Jaunsars and placed them as younger than the Simlas. He has recognised within the Jaunsar formation the following three subdivisions in normal sequence.

C. The Chandpurs and Nagthats between Bansa and Juini Dhar.

B. The Bansa Limestone, a thin band near the village Bansa, south-west of Sayasu.

A. The Mandhalis between Sayasu and Bansa.

Confining our attention mainly to the Sirmoor territory and particularly to the Shillai Hills south-east of Chandpur, the 'Mandhalis' are found to consist largely of hard slates, dark, reddish gray or violet in colour. They are frequently arenaceous and coarse-bedded and pass into hard sandstone bands. Not infrequently do we come across a few quartz veins traversing obliquely to the bedding planes, whereas the conglomerates are quite infrequent. The slate and sandstone beds are highly folded, faulted and sometimes sheared and occur generally with very steep dips. The general strike is N N W—S S E.

Near the Tons between Sayasu and Senj these are in direct contact with the Nummulitic limestones over which they lie with violent discordance, the Tons Thrust of Auden. The underlying limestones have generally low dips to the south-east whereas the overlying slates are nearly vertical with a strike at right angles to that of the limestones. These discordant relations are very clearly seen near Anyar on the Tons west of Senj. The dark compact slates with their arenaceous facies have all the characters of Simla Rocks as typically seen on the Giri near Duddham. Pilgrim and West also had recognised the Simla character of these Mandhalis near the Tons.[3]

The Simla type of rocks are very prominently developed between Sayasu and Bansa as also between Sayasu and Bhatwar east of Chandpur.

At Bhatwar we see these rocks being overlain by thinly bedded olive shales and phyllites in all respects similar to the Infra Krols. These rocks continue northward through Burek, Dharwa, Jakandon to Naihna-Sakhaoli and possibly beyond. South of Dharwa these rocks are gently folded and are fairly free from plication but north of Dharwa they show an increasing degree of disturbance until at Naihna the slates are extremely folded and plicated yielding some of the finest hand specimens exhibiting these structural features on minute scale.

This band of Infra Krol type of shales and slates continues S S E of Bhatwar and is seen near Bansa, Bobri and Kandaria directly overlying the Simla type of rocks. Here the outcrop is quite well marked though not quite so extensive as in many other places. The nature of the shales, their colour and their mode of weathering are typical of the Infra Krol shale, and for this reason they were already correlated with the Infra Krols by Pilgrim and West.[4]

Bansa Limestone

These are succeeded by a limestone band marked by Auden as Bansa Limestone which is shown in his map of the Krol Belt as running N W—S E from near Bandil through Bansa, Bobri—towards Salia on the Kalsi-Chakrata Road. The Limestone band is thin though fairly prominent in

the topography of the region. It is a hard gray limestone somewhat with a striped and banded appearance but otherwise quite similar to the Krol limestone. In a private communication Auden pointed out that it is highly siliceous whereas the normal Krol limestone is not. Looking, however, to its association with shales of undoubted Infra Krol nature which in their turn are lying over the Simla type of slates the correlation of this thin limestone band with the Krols is irresistible. We may at best regard it as a slightly varied facies of the Krol limestone.

A thin limestone band was noted a little east of Kando-Bhatnol resting over the Infra Krol shales roughly with a N—S strike. Though slightly pinkish in appearance this band is evidently the northern continuation of the Bansa limestone. Very much the same type of pinkish limestone was also observed a little north of Naihna-Sakhaoli towards Koti-Singtau. Here was however a much wider outcrop again associated with Infra Krol shales, and may be a continuation of Deoban Limestone of Krol affinities. Thus it would be seen that what has been noted as Bansa limestone, though at places slightly varying in facies, has distinct Krol affinities and association.

When we move west from Bansa towards Pashmi and Matyana we again find the repetition of shales and slates of typical Infra Krol and Simla facies in much wider exposures forming the western limb of the syncline.

About half a mile west of Matyana the Simla type of slates are overlain by a thick series of quartzites of the typical Jaunsar formation with a distinct thrust plane running between the two (Fig. 1).

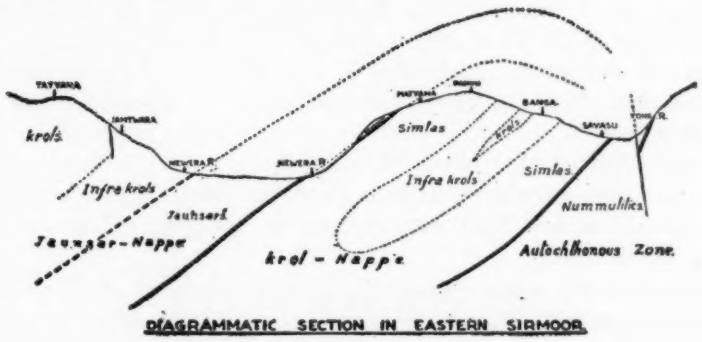


FIG. 1

Thus we see that what Auden considered as a single Jaunsar formation extending from the Tons to the Juini Dhar actually consists of two distinct units separated by a thrust plane and that what was considered as Mandhalis

is properly the Simla-Infra Krol sequence with the Bansa Limestone as equivalent to Krol-limestone.

This Simla-Infra Krol-Krol sequence of the Shillai syncline belongs to an independent tectonic unit: it is underlain by the Nummulitics possibly of the autochthonous zone while upwards it is thrusted over by the Jaunsar Nappe. In these respects the Shillai syncline corresponds very closely in its tectonic position with the Krol syncline of the Solon-Dadahu region and thus belongs to the Krol Nappe proper.

Jaunsar Formation

Having thus seen that the Mandhalis do not belong either stratigraphically or tectonically to the Jaunsars the only lithological elements now left within the Jaunsar system are:

(*a*) the Chandpur quartzites and phyllites and (*b*) the Nagthat arkoses, sandstones and conglomerates. Since according to Auden the Nagthats are not represented to any large extent within the confines of the Sirmoor State it is not intended to deal with them here. It is the Chandpur facies alone which strictly speaking is the characteristic Jaunsar element present within the Sirmoor Hills.

The principal outcrops of the Jaunsar series are confined to two linear strips. One runs roughly along the northern bank of the Giri from beyond Ranaghat, Dharoli and Chakhal on the western boundary of the State to almost near Sataun where the Giri takes a sudden bend to the south to join the Jumna. The other outcrop starts roughly from near Naihna on the north-eastern boundary of the State and runs along the Chandpur-Shillai range down to the Tons and beyond, into the Kalsi region. The two outcrops are continuous underground and form a synclinal basin. The western outcrop of the Jaunsars near Karganu and Duddham rests over the Simlas along the Giri with a strong thrust plane represented by an intervening thick band of the so-called Blaini boulder bed. A little to the south-east, near Siyun the same Jaunsar formation comes to lie successively on the Infra Krols and Krols and even crosses the synclinal axis of the Krol basin to the south.

Much in the same manner the eastern outcrop of the Jaunsars along the Chandpur-Shillai Range also comes to lie on the different members of the Simla-Krol sequence, the so-called Mandhalis of Auden. Here, between Naihna and Kando-Bhatnol north-east of Chandpur, one observes one of the finest field illustrations of the Nappe structure. The soft grayish olive shales and slates of the Simla-Infra Krol sequence, intensely folded and plicated, form the lower slopes of the hills, whereas the top regions are

composed of very hard quartzites of the Jaunsar series. The resulting topography is generally very rugged and precipitous and landslides are fairly common.

The same band of Jaunsar quartzite is again observed in the Neweli river west of Matyana where it lies thrusted over the Simla slates but about two miles to the west it is seen to dip at high angles to the S.W. below the Infra Krol-Krol sequence. At the junction an intervening thick layer of " Blaini " breccia bed has been developed (Fig. 1). The Jaunsars are thus not an upward continuation of the Mandhalis nor of the Simlas but represent a distinct and much older stratigraphic unit resting over them as a higher tectonic unit—the Jaunsar Nappe.

The Chail Series

The extensive formation of variegated shales, slates and phyllites exposed over the Jaunsar quartzites between Pitli, Chayal and Rajgarh in the western Sirmoor have been mapped by Pilgrim and West as Chail series. The same formation continues with variable thickness to the south-east through Piriyaghat and Ludhiana to Pulilanighat. It was apparently this development of the formation which led Pilgrim and West to differentiate it from the Simlas on account of their higher degree of metamorphism and to regard them as older than the Jaunsars. The author had an opportunity of examining these rocks in the field both in the western part, between Pitli and Rajgarh and in the eastern part between Ludhiana and Jablog and the most striking impression left on his mind was their extreme similarity partly with the Infra Krols and partly with the Simlas. In certain places the shales are so soft and crushed that they have led to extensive land sliding as at Ludhiana. They show no appreciable metamorphism and often weather like Subathus into tiny pencil slates and angular fragments. Only in the upper parts do we meet with compact dark slates of typical Simla facies such as those between Andheri and Olong on the Rigana Dhar and those near Jablog, Chabdhar and Kujwa.

These " Chails " rest on the Jaunsars with a northerly dip but it appears very probable that here we are dealing with a series of shales and slates apparently in an inverted sequence or in a highly squeezed syncline with a core of Infra Krols (Fig. 2).

It appears therefore more plausible to regard the Chails as only Simla-Infra Krol sequence belonging to the Jaunsar Nappe.

West has more recently studied the rock formations in the Shali region north-east of Simla and has come to the conclusion that the Chails are identical with Simlas.[5]

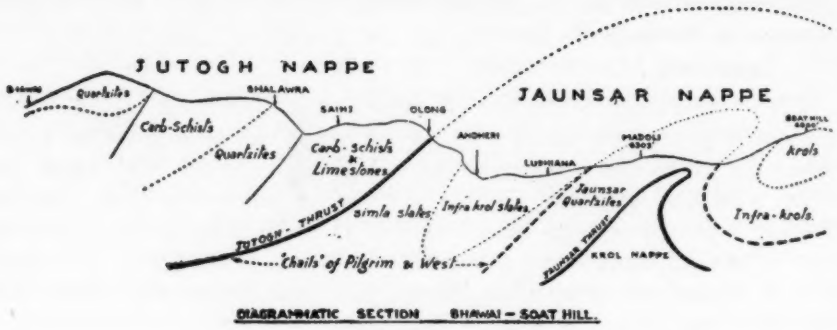


FIG. 2

The "Lower" Tals

In his description of the Krol Belt Auden has newly introduced a "Lower Tal" series to describe a thick series of carbonaceous shales, slates, phyllites and greywackes found resting over the massive Krol limestone in the Koti-Dhaman (Nigali-Dhar) and Salag Synclines in eastern Sirmoor. Auden had originally considered this series as Infra Krol from the general look and lithological characters but the fact that they lie over the Krols without apparent unconformity led him to recognise in them a completely new series which he called "Lower Tals" and regarded it as younger than the Krols and in proper sequence. The difficulties of correlation have to be admitted in a highly disturbed region such as the Himalayas, particularly when we have to deal with unfossiliferous formations. But of the two factors—lithological characters and field succession—it is undoubtedly unsafe to rely entirely on the field sequence to the neglect of lithology. In these disturbed parts Auden appears to have given preference to the superposition in regarding these so-called "Lower Tals" as younger than the Krols and he has disregarded the evident lithological similarity with the Infra Krols which he had originally recognised.

The only formation known in the outer Himalayas as younger than the Krols but older than the Subathus is what is known as the Tal series of Garhwal which Medlicott originally discovered in the Tal valley east of the Ganges. The rock types of the Tal valley as described by Middlemiss consist of "grits or quartzites—frequently calcareous and in places pass into limestones which contain fragmentary, indeterminate fossils of the Oyster type of possibly mesozoic affinities."

The shales, slates, phyllites, and greywacke resting over the Krols of the Koti-Dhaman and Salag synclines have been correlated with the Tals

with which there is not the slightest lithological similarity, let alone the total absence of fossils in the former.

These have been distinguished by Auden as "Lower Tals" for which there are no equivalents in the type locality in Garhwal.

It has been observed that these argillaceous beds are lithologically very much similar to the Infra Krols and Simlas. They however lie over the Krol limestone but the junction as observed by the author at Thontha south of Tatyana is far from normal and is distinctly disturbed and partly even thrusted.

It has to be emphasised that there is no need to assign a younger age to these beds merely because of their apparent conformable position over the Krols. In the field these beds contain elements of Infra Krols and Simlas possibly in an inverted sequence as if through overfolding of a syncline and simultaneous thrusting.

In this it is not altogether improbable that what we see as the normal sequence of Infra Krols and Krols above the Jaunsar quartzites represent the lower limb of the syncline, while the upper limb composed of Infra Krols and Simlas has been turned over and partly thrusted over the Krols. In this respect the overturned limb with Infra Krols and Simlas in the inverse order would actually represent what has been termed the 'Lower Tals'.

Similar reversed synclinal limbs have already been recognised in connection with the so-called "Chails" of Ludhiana—Olong section—which also rest over the Jaunsars and occur almost in continuation with the "Lower Tals" of the Koti-Dhaman-syncline.

We can then put forward the following correlation.

	Pulilanighat		Nigali Dhar		
Jaunsar Nappe	Chails	Simlas Infra Krols	Simlas Infra Krols	Lower Tals	Inverted upper limb of Simla-Krol syncline
		Infra Krols Simlas (not well developed)	Krols Infra Krols Simlas (not well developed)		Normal lower limb
	Jaunsar Quartzites and Talc Schists				
	"Jaunsar Thrust"				

The "Upper Tals"

The two synclines in the eastern Sirmoor—the Koti-Dhaman (Nigali Dhar) and Salag—also contain some rock types which have led Auden to introduce, beside the "Lower Tals", one more series not known

anywhere else throughout the Simla-Sirmoor-Chakrata region. These are the "Upper Tals" which Auden considers to correspond best with the quartzites of the type locality in Garhwal already referred to and to which he assigns a mesozoic age.

The rocks in Tal Valley of Garhwal include, as already stated above, grits or quartzites which are associated with limestones containing fossils of mesozoic affinities. It is maintained that since the limestones lie conformably over the Quartzites the two formations belong to one and the same formation called the Tals of Mesozoic age. It is curious how the quartzite, a highly metamorphosed rock, altogether devoid of fossils, could be of the same age as the overlying unmetamorphosed fossiliferous limestone simply because no unconformity has been noticed between the two. The possibility exists that the conformable junction between the two rock types in the Tal Valley is only apparent and that the two belong to quite different ages and to two different tectonic units brought together by thrust movements.

From the Oyster type of fossil contents the limestones of the Tal Valley appear to be not much older than the Nummulitic limestones and may possibly represent a lower part of that series. The quartzites, on the other hand, which underlie them appear much older—and may be even precambrian.

If this were granted it would be proper to correlate the quartzites of the two Sirmoor synclines with the quartzites of the Tal Valley without assigning the Tal (Mesozoic) age.

The quartzites of the Koti-Dhaman area are highly metamorphosed and recrystallised. They show some similarity with the Jaunsar Quartzite with which they were first correlated by Middlemiss and Auden, but on the basis of some lithological differences which are fairly obvious Auden later considered them to be quite distinct and correlated them with the quartzites of the Tal Valley.

On the other hand if we take the quartzites of the Koti-Dhaman as Upper Tal of Jurassic age and in proper sequence over the Krols and Lower Tals as suggested by Auden it is surprising how these Tals should be altogether absent from all other parts of the Simla-Sirmoor-Chakrata region. We have the most complete development of the Krols in the Krol belt but in this not a trace of these Tal beds is to be found. Again, these Tals are nowhere seen in contact with the Subathus, while if the sequence Krol-Tal-Nummulitics were a true and a normal succession they should have been found together. Auden maintains that the sequence Blaini-Infra Krol-Krol-Tal is "normal" in the sense that they are in their original order of

deposition and are unaffected by thrusts and he further proposes that the above sequence may be taken as the standard of reference for the Krol Belt. When it is realised that the two synclines of Koti-Dhaman and Salag—do not belong to the Krol Belt proper but to the higher tectonic unit, the Jaunsar Nappe, the " normal " succession as suggested by Auden just fails in the Krol belt for which it was proposed as a standard.

From their absence throughout the Krol region it is evident that these " Upper Tal " Quartzites are an element altogether foreign to the Krol sequence. They do not correspond even to the Jaunsars in their lithology; they are much harder and purer types of quartzites showing recrystallization into coarse-grained, white pinkish or greyish, gritty or massive rocks quite free from the argillaceous admixture. The Jaunsars on the other hand are dark, fine-grained and in many cases highly slaty approaching quartzitic slates and show no appreciable recrystallization.

The only rocks with which the Koti-Dhaman quartzites show any similarity both in composition and in degree of metamorphism are the Jutogh quartzites of northern Sirmoor.

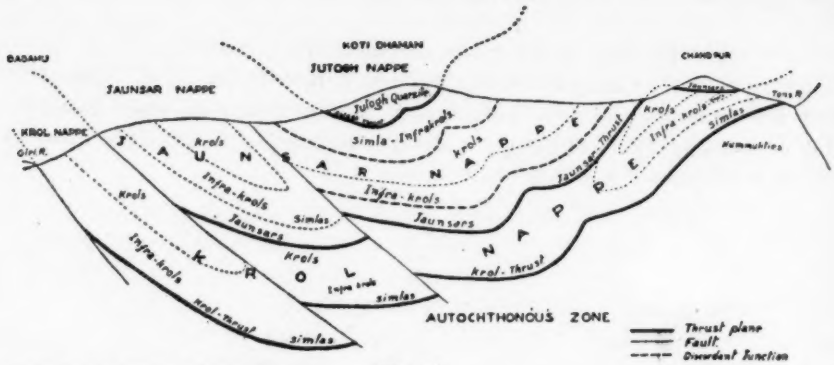
The Jutogh quartzites cover the largest part of the region between the Chor Granite and the Giri and overlie with a strong thrust (the Jutogh Thrust), the Infra Krols and Simlas (Chails of West) of the Jaunsar Nappe all along their western and southern boundary.

It has already been noted above that the " Lower Tals " of the Koti-Dhaman and Salag synclines are only the inverted and possibly thrusted limbs of the Krol synclines in the Jaunsar Nappe and correspond largely to the " Chails ". It is therefore natural that the Jutogh quartzite which is so consistently occurring thrusted over the Chails all along the extensive belt in Sirmoor should also be found in the corresponding position over the so-called Lower Tals of these synclines, which are only a southern continuation of the " Chails ".

The quartzites of the Koti-Dhaman and Salag synclines thus represent the Klippen remnants of the Jutogh Nappe resting over the Jaunsar Nappe (Fig. 3).

The Guma Thrust which has been noted by Auden along the northern part of the Koti-Dhaman syncline also coincides largely in its position with the Jutogh Thrust in this syncline.

The following table would indicate the differences between the two interpretations of the sequences and tectonics of the central Sirmoor region.



DIAGRAMMATIC SECTION DADAHU—CHANDPUR FIG. 3

According to Auden		Koti-Dhaman-Sayasu Section	According to Rode	
Nappe	Series	Rock types	Series	Nappe
	Upper Tal	Quartzites	Jutogh	Jutogh Nappe
	Lower Tal	Graywacke Phyllites and Shales	Simla Infra Krol	
	Krol Infra Krol	Limestones Shales	Krol Infra Krol	Jaunsar Nappe
Krol Nappe	Nagthat Chandpur	Slates Quartzites	Simla Jaunsar	
	Bansa	Limestones	Krol	
	Mandhali	Shales and Phyllites (Conglomerates)	Infra Krol and Simla	Krol Nappe
Autochthonous	Nummulitic Simla	Limestones, Shales Slates, etc.	Nummulitic Simla	(? Para-) Autochthonous

Thus the Krol Nappe of Auden is divisible into three independent Nappes: (*a*) Krol Nappe, (*b*) Jaunsar Nappe and (*c*) Jutogh Nappe.

Extent of the Jutogh Thrust

The same phenomenon of the Jutogh Klippe as is here indicated for the above two synclines has also been found in Garhwal where Auden has described the outliers of Banali, Satengal, etc., as Garhwal Klippe.[6] Here Auden notes the occurrence of Schists resting over what he calls the Tal quartzite which in its turn is found to overlie the shales and limestones of the Krol sequence.

He separates the schists from the underlying quartzites by a thrust which he calls the Garhwal Thrust, while he combines the " Tal " Quartzites with the underlying—Lower Tals, Krols, Blainis, Nagthats and Chandpurs and constitutes the Krol Nappe. His interpretation for the Banali outlier has been illustrated in Fig. 4.

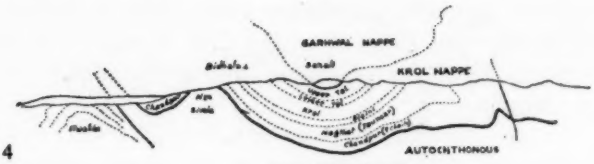


FIG. 4

THE GARHWAL NAPPES

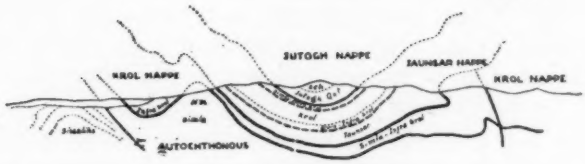


FIG. 5

THE GARHWAL NAPPES

Reinterpreted by K.P. Rose.

Though the present author is not conversant with the Garhwal area personally, he sees the possibility of a different interpretation of this sequence, which is in keeping with the ideas developed in the study of the Sirmoor Himalayas. The new interpretation has been illustrated in Fig. 5. It is here suggested that what are termed as Tal Quartzites have nothing to do with the underlying Krol sequences nor with the Krol Nappe but that these quartzites together with the overlying schists constitute the Jutogh Nappe. The tectonic correlation in this region comes out exactly similar to what we find in the Sirmoor Himalayas as given in Table 1.

If this interpretation were accepted the Garhwal Nappe, with its schists and the underlying quartzites, becomes equivalent to the Jutogh Nappe. Auden dismisses the Jutogh Thrust as being absent *everywhere* except at Simla where the Thrust was recognised by Pilgrim and West. West appears to have agreed with this view, for he accepted that the Jutogh Thrust may not be of significance towards south-east.[7]

A study of the Chor region has impressed the present author with the remarkable persistence and magnitude of the Jutogh Thrust all along the foot of the Chor Hills from Chayal and Rajgarh in the west to Jablog and

Chabdhar on the south. The Jutogh quartzites stand out with rugged boldness against the soft shales and slates of the "Chails" which show signs of enormous structural disturbance at the contact.

The Jutogh Thrust is a very important tectonic feature of the Sirmoor Hills and may possibly continue to be so to the south-east though with a lesser prominence. It seems therefore quite likely that what Auden considers as a Garhwal Nappe is only a continuation of the Jutogh Nappe passing through Koti-Dhaman and Salag synclines and possibly through north Kalsi-Lakhwar tract and finally extending through Landour Cantonment to the Satengal outcrop.

The Chor Granite

Lastly we come to the interpretation of the granite masses such as those occurring at Chor, Lansdowne, Almora, Dudatoli, Dwarhat, etc. According to Auden[8] these granite masses are intruded into phyllites of one type corresponding to the more metamorphosed facies of the Chandpurs and have induced contact metamorphism into the latter leading to the formation of Garnet-Chlorite-Schists, Biotite Schists, etc. These schists are supposed by him to be distinct from the Jutogh Schists of Simla region which according to him belong to a higher series. There is probably some confusion here since the Inner Schistose Series is not identical with, nor is it a metamorphosed equivalent of the Chandpurs unless we revert to Meddlicott's views regarding the correlation of these rocks. Again the granites have induced no contact metamorphism in the schists which are in the largest part only dynamically metamorphosed older sediments. A clear evidence of this is seen at Chog-Tali in the Chor Hills where a large bed of crystalline limestone occurs within a few yards of the granite mass without showing any contact effect. On the other hand garnetiferous-mica-schists are seen well developed several miles away from the nearest granite mass.

The granite of the Chor Hills is coarse-grained, porphyritic with large crystals of feldspar often irregularly oriented, and is in places altogether free from metamorphic effects. More frequently, however, the granite is distinctly gneissose with a parallel arrangement of the large feldspar phenocrysts. It is even foliated into schistose granite. In certain localities granite masses show abundant inclusions of mica schist without showing any resorption. In the outer and possibly also in the basal parts of the granite mass a highly foliated schistose variety is developed on a very large scale. This may be taken as granite-porphyry schist. Except for the absence of garnet and frequent presence of feldspar phenocrysts the porphyry schist resembles very much the mica schist of the Jutogh series over which it rests and from which it is sometimes difficult to distinguish.

The zone of granite porphyry schist is abundantly traversed by tourmaline-mica-pegmatites often of large dimensions. This zone is also traversed by large doleritic dikes and sheets extending for long distances.

The whole field evidence indicates a large-scale movement of the granite mass over a sheath of granite prophyry schist and basic trap sheets which probably served as zones of slipping.

The Chor granite as also that of Lansdowne, Almora, etc., is in the nature of a Klippe of the central Granite Thrust resting over the Jutogh formation. This Granite Thrust is the highest tectonic element present in the Sirmoor Hills.

Nappes in the Simla-Sirmoor-Himalayas

The observations in the foregoing pages lead us to the recognition of various tectonic elements in the Sirmoor-Simla Himalayas as set forth in the following scheme. This scheme appears to hold good for many other regions of the Himalayas south of the Central Axis.

Table 1. *Tectonic Correlation of Simla-Sirmoor Formations*

Granite, gneissose Granite, Gneiss Granite-porphyry schist with Pegmatites and Dolerite Sheets	Central Crystalline Nappe
Garnetiferous mica-schist-Limestones and Boileaugunge Quartzites (including ' Upper Tals ')	Jutogh Thrust
Infra Krols and Simlas (including Chails and ' Lower Tals ') Krols Infra Krols Simlas Jaunsar Quartzite (including Chandpurs)	Jaunsar Nappe (Shillai and partly Giri Thrusts)
Krols (including Bansa Limestone) Infra Krols } (including Mandhalis) Simlas }	Krol Nappe (Tons Nappe)
Dagshai Subathus (including Nummulitics) ? Simlas	Parautochthonous and Autochthonous Zones

It may be noted here that the time sequence of these various thrusts is in the reverse order of their succession so that the Central Crystalline Thrust represents the earliest tectonic phase whereas the Krol Thrust represents the last major phase. There have been subsequent thrust movements but they are comparatively less significant.

Stratigraphic Succession of the Simla-Sirmoor Rocks

Having studied the various rock-formations in different parts of the Sirmoor Hills in the proper perspective of lithological characters, order of superposition and their associations in different tectonic units, we are now

in a better position to arrange the various rock-types in a more appropriate order of stratigraphic succession. Since the rock-types in the Sirmoor region are identical with and are largely in continuation with those in the Simla region the succession arrived at for Sirmoor rocks will also apply equally to the Simla rock-formations. When, however, we attempt to correlate these unfossiliferous formations with the standard stratigraphical scale we are immediately faced with difficulties in the absence of reliable evidence. Since the time of Oldham the Blaini Boulder Bed was taken as a datum bed for assigning ages to the associated rock formations but the present author has shown elsewhere[9] that the Blaini bed is largely a tectonic formation having no stratigraphic significance and hence we are not justified in using it for stratigraphical purposes. We have no other evidence to rely upon. It further appears to the author that, the degree or extent of metamorphism one observes in the various rock-formations in these Himalayas does largely represent the pre-Tertiary, dynamo-regional, metamorphism, and is only slightly modified by the Himalayan orogenesis. The contact metamorphism of magmatic intrusions also is strictly limited in space and has not contributed appreciably to the general metamorphic condition of the various rock types.

With these considerations in view the author proposes the following scheme of stratigraphic succession and correlation for the Simla-Sirmoor rock-formations. In this the age relationships are not very different from those suggested by Holland. The succession of major rock-formations follows the one adopted by Pilgrim and West, while the correlation of the minor series has been adopted for the first time here.

Table 2. *Stratigraphic Succession and Correlation of the Simla-Sirmoor Rock-Formations*

Formation	Major lithological types	Equivalents	Age
Alluvium, Land-slides		..	Recent
Siwalik	Sandstones, Clays, Conglomerates		Mid-Upper Tertiary
Blaini	Tectonic Conglomerates and Breccia	..	Middle-Tertiary and older
Dolerite dikes, sheets and Quartz Porphyry		..	"
Dagshai	Sandstones and Clays	..	Lower Miocene
Subathu	Limestones and Shales	Nummulitics	Eocene-Oligocene
Krol	Limestones, Shales, etc.	Bansa Limestone, Deoban "	Vindhyan ; Lower Palæozoic to Pre-Cambrian
Infra Krol	Shales and Phyllitic Slates	Lower Tal "	
Simla	Slates	Chail, Mandhali	
Jaunsar	Quartzites and Talc Schists also micaceous	Nagthat	Purana (Cuddapah)
	Slates with Quartz veins	Chandpur	
Jutogh	Chor Granite and Gneisses, later recrystallised. Dolomitic Marble ; Garnitiferous-graphitic-, pyritous-, mica Schists and Quartzites ; with intrusive Hornblende Schists and Gneisses	'Upper Tal'	(Delhi, Raialo and Aravalli) Archæan

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